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On the Morphology of the Compound Eyes of Arthropods.

by

S. Watase,
Bruce Fellow in Biology.

Presented as a Thesis to obtain
the degree of 'Doctor of Philosophy'
at the Johns Hopkins University.
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ON THE MORPHOLOGY OF THE COMPOUND EYES OF ARTHROPODS.

By S. WATASE, Fellow of the Johns Hopkins University. With Plates XXIX–XXXV.

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I.—INTRODUCTION.

Early in the spring of 1888, Prof. W. K. Brooks kindly placed at my disposal a valuable set of specimens of *Limulus*,[1] with a suggestion that I should work on the eyes in order to continue the research upon which the late Dr. A. T. Bruce was engaged at the time of his death.

Through the kindness of Prof. M. McDonald, the United States Commissioner of Fish and Fisheries, I was enabled to continue my work on the subject during the summer of the same year at the Woods Holl Laboratory of the Fish Commission, where the fresh specimens for the study of *Limulus* at all stages of development may be obtained without difficulty. To these gentlemen are due my sincere thanks and gratitude; through their kindness and encouragement I have been enabled to prosecute my

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[1] These specimens were mostly preserved by Dr. J. C. Hemmeter, when the Chesapeake Zoological Laboratory was in session at Beaufort, N. C., in 1885. They were in an excellent state of preservation.

work. I am also indebted to Prof. John A. Ryder and Dr. E. A. Andrews for various courtesies.

It soon became evident that the eye of *Limulus* is, as we might expect from its great antiquity, a very primitive visual organ, presenting in a simple form a most interesting type.

For the further comprehension of its structure and significance it became necessary to extend my researches to several other Arthropods. Among the forms studied in this connection are the following, besides five other pelagic Arthropods from the Gulf Stream, whose generic names have not yet been ascertained: *Branchipus*, *Estheria*, *Talorchestia*, *Hyperia*, *Phronima*, *Serolis*, *Ligia*, *Asellus*, *Notonecta*, *Libellula*, *Agrion*, *Gryllus*, *Corethra*, *Cambarus*, *Homarus*, *Hippa*, *Alpheus*, *Gebia*, *Penaeus*, *Squilla*, *Callinectes*, *Gonodactylus* and *Lucifer*.

While only a few selected types are here described, all the above named forms, representing three great groups of Arthropods, Insects, Crustacea and Arachnids, were carefully studied, and all the results have been embodied in the general observations which follow, although the principal subject of the paper is the eye of *Limulus*.

The points which are at present receiving marked attention among the workers on the morphology of the compound eyes of Arthropods may be put in four principal categories, viz. (1) the mode of termination of the optic nerve fibre in the retinal cell; (2) the mode of formation of different "layers" in the retina; (3) the phylogeny of the compound eye; and (4) the homology of the optic ganglia.

The problem therefore involves several inquiries. The fundamental step is to determine to what morphological category the compound eye of the Arthropod belongs. To the elucidation of this point our histological inquiries must be directed, while our phylogenetic consideration of the eye may fitly be reserved until we have learned something of its structure.

The first thing which confronts us is this: What is the ommatidium or "eyelet," the repetition of which, often several thousandfold, gives rise to the compound eye? What is the significance of the characteristic arrangement of its component cells? Is it possible to reduce it to a simpler form, or to express its structure and significance briefly?

Until these questions be answered satisfactorily, the most laborious technique of histology is often powerless to discriminate the essential from the secondary features in the component cells of a given ommatidium; and in the absence of an accurate conception of its fundamental structure, the various modifications of the cells and fibres of an ommatidium may be made to assume any significance to suit our speculative ideas.

With these considerations in mind, I have sought for an ommatidium in which all the features of its structural elements may be made out plainly, and from which we may derive the ommatidial elements of a more complex type.

Although the number of forms studied in this connection is not quite so extensive as I wish, I feel justified in believing that any view which explains the structural peculiarities of the ommatidia of each and all of the forms in the list above given and reduces them to the same fundamental structure, may fairly be considered as in all probability generally applicable to the eyes of Arthropods.

In what follows, the attempt will be made to approach the subject from this standpoint, viz. the consideration of the ommatidium as the morphological unit of the compound eye in Arthropods, just as each little circle of rods with a cone in its centre may be considered as the morphological unit of the "mosaic layer" (Henle) of the human retina.

II.—The Morphology of the Ommatidium.

Following the plan given in the Introduction, I will consider the morphology of the ommatidium, taking it as the structural unit of the compound eye. After the nature of this unit has been considered, we may proceed to examine the state of aggregation of the units in the different forms of the Arthropods. For this purpose it is convenient to select one particular ommatidium which may be made the basis of comparison. Accordingly, the ommatidium of *Serolis* will be considered at the outset, and the attempt will be made to homologize the ommatidial elements of *Serolis* with those of other forms. I am indebted to Prof. M. McDonald for the opportunity to study the eyes of the four South American forms of *Serolis* recently brought back by the U. S. Fish Commission steamer *Albatross*.

a. Serolis.

(Figs. 1, 1*a*, 1*b*, 2, Pl. XXIX.)

The general structure of the eyes of *Serolis* has already been made known by Beddard.[1] Although I have verified all the chief results of his research, I shall speak of a few details which seem to me specially significant.

The cells of the ommatidium are arranged in three principal strata, *a*, *b*, *c* (Fig. 1*a*, Pl. XXIX). Each stratum of cells is characterized by the special product which it secretes, viz. 1, 2 and 3.

The outermost stratum (*a*) secretes upon its external surface the chitin which constitutes the *cornea* or the *corneal facet* (*c*, Fig. 1, Pl. XXIX).

The cells themselves have been designated as the *corneagen* by Patten.[2]

The corneagen is sometimes difficult to detect in the eye of the adult animal and may easily be overlooked. It is very conspicuous in the young.

The next stratum of cells (*b*) is also characterized by the chitinous secretion on the surface nearest the median axis of the ommatidium. The two cells (*b*) secrete a thick chitinous layer which encloses an ovoidal space of considerable size filled with a transparent liquid substance, (2). The cell (*b*) has been named *vitrella* (Lankester and Bourne);[3] and the ovoidal chitinous body (2) is the *crystalline cone*[4] (*c. c*, Fig. 1, Pl. XXIX.)

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[1] Beddard, F. E. Challenger Report, Zoology. Vol. XI, *Isopoda: Serolidae.* His additional observations on *Serolis* may be found in the paper by the same author, *On the Minute Structure of the Eye in Cymothoidae*, Trans. Roy. Soc. Edin. 1887.

[2] *Studies on the Eyes of Arthropod: I. Development of the Eyes of Vespa, with observations on the Ocelli of some Insects*, p. 193, Journal of Morphology, Vol. 1, No. 1, 1887.

[3] *The Minute Structure of the Lateral and the Central Eyes of Scorpio and Limulus.* Quart. Jour. of Micro. Science, Vol. XXIII, p. 198, 1883.

"Vitrella" is synonymous with "retinophora" of Patten; "vitreous cell" and "crystalline cone cell" of authors. The nucleus of the vitrella has been named by Claparede "Semper's nucleus," aftet its discoverer: *Zur Morphologie der zusammengesetzten Augen bei den Arthropoden.* Von Edouard Claparède. Zeit. f. Wiss. Zool. Bd. X, p. 193, 1860.

[4] It is interesting to notice that the observations made by Clarke on the eye of a Trilobite (*The Structure and Development of the Visual Area in the Trilobite,*

The crystalline cone is purely a dioptric apparatus. A careful study of its structure, both in the adult and in the young embryos of *Serolis*, has clearly shown that this has nothing to do with the sensory function, as it has no connection whatever with the optic nerve fibres.

The vitrella, then, agrees with the corneagen cell in the capacity for secreting chitin on one portion of its surface. The difference between them consists in this, that while the corneagen cells secrete chitin towards the exterior of the body, the vitrellae secrete it towards each other, that is, towards the median axis of the ommatidium.

Next below the vitrella comes the important stratum (*c*, Fig. 1*a*) which lies at the bottom of the whole structure, and which sends processes inward (*Op. n*) to form the optic nerve fibre, which terminates in the optic ganglion.

The cells in this structure are also characterized by secreting chitin towards the median axis of the ommatidium. The chitin thus produced invests the colorless portion of the cell (*c*) constituting the rod or the *rhabdomere* (Lankester and Bourne).[1]

A large number of transverse striae, running at right angles to the longitudinal axis of the ommatidium, are seen through the transparent cuticle. The cell itself which gives rise to the rhabdomere has been known as *retinula* (Grenacher).[2] The

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Phacops Rana, Green, Journal of Morphology, Vol. II, No. 2, 1888) show, so far as I understand his account, that the lens has a somewhat similar structure to the crystalline cone of *Serolis*, or, in fact, to the crystalline cone of Isopod crustacea, as far as it is known. From Clarke's description I gather *that the lens of Phacops is unequally biconvex, the curvature being the greatest on the proximal surface; and that the lens was hollow, probably filled with some viscid humor.* In the absence of a more complete knowledge on the nature of a corneal covering to the eye in the Trilobite it is premature to carry out the homology of the "crystalline cone" of *Serolis* and of the Isopods in general to the "lens" of a Trilobite, although there appears to exist a certain resemblance between the two. It is perhaps worthy of mention, in this connection, that there is nothing whatever in the lens-cone of *Limulus* at any period of its development which shows any resemblance to the lens of a Trilobite as made out by Clarke. *The lens-cone of Limulus is the solid, conical projection of the chitinous cuticle of the body, fitting into the open depression of the skin, and in no period of the life history of the animal is it separated from the outermost cuticle of the body.* (Compare Grenacher, Lankester and Bourne, and Part III of the present paper on the compound eye of *Limulus*.)

[1] *loc. cit.* p. 183.

[2] *Untersuchungen über das Sehorgan der Arthropoden*, 1879.

retinula, then, agrees with the corneagen and vitrella which lie above, in its capacity to secrete chitin on a part of its surface. Thus the three strata of cells, *a*, *b*, and *c*, agree fundamentally with one another in their capacities to secrete chitinous structures, and these are respectively known as the *cornea* (1), the *crystalline cone* (2), and the *rhabdomere* (3).

Hence, aside from the general homology which exists between the cells in the optic area, all being derived from a common source, the ectoderm, there exists a special homology between the cells in the three strata which constitute the important parts of the ommatidium, all being characterized by the capacity for secreting chitin from a part of their surface.

In this respect these ommatidial cells are essentially like the general ectodermal cells which secrete the chitinous covering of the body from their distal extremities.

In carrying this analysis further we find that the outer surface of the corneagen is homologous with the axial surface of the vitrella, and that of the retinula and the three chitinous structures, *cornea, crystalline cone* and *rhabdomere*, are homologous with each other.

If this interpretation be established by the further discussion of the ommatidia of other forms, it follows that the crystalline cone and rhabdomere are really homologous with the chitinous investment of the body, and the narrow axial space of the ommatidium represented by the line x must therefore have the same significance as the space outside of the body. Morphologically speaking, the crystalline cone and rhabdomere are just as much a part of external surface as the cornea itself. Diagramatically, the three strata of the ommatidium may be represented as in Fig. 2, Pl. XXIX.

According to this view, the ommatidium of *Serolis* may be regarded as an open pit of the ectoderm, the walls and margin of which are covered by the product of their own secretion, the chitin. The chitin in the walls and margin of the pit becomes continuous with the general chitinous covering of the body, as the rows of the ommatidial cells themselves become continuous with the general ectoderm.

At the bottom of the ommatidial pit there exists a pair of colorless "hyaline cells" (Beddard), with their upper processes

inserted into the axial space between the four rhabdomeres. Each cell has a peculiar refractive nucleus. It lacks any connection with the optic nerve fibre, and is suspended from the bottom of the pit at a considerable distance above the basement membrane. The "hyaline cell" is a modified ectodermic cell, and is homologous with the rest of the cells which enter into the formation of the ommatidium. The cell, however, does not develop pigment granules in itself, nor establish any connection with the central nervous system as does the retinula cell, nor does it secrete chitin on a part of its surface as do the rest of the ommatidial cells we have considered already. As to the function of this cell I am not able to say anything definitely. It cannot be sensory, having no connection with the nerve centre. When we see, however, that in some species of *Serolis* the lower ends of the four rhabdomeres are deeply imbedded in the substance of the "hyaline cell," or, in other words, that the rhabdomeres are firmly held together by the substance of the "hyaline cell" at the point where they meet, it becomes probable that the cell in question may serve the purpose of a mechanical support, adding firmness to the whole structure. To this point I will recur later on.

In addition to the cells which form the essential part of the ommatidium there exists a number of pigmented cells, (*pg. c.* Fig. 1*a*, Pl. XXIX). The pigment cells are greatly developed around the vitrellae and closely invest the dioptric portion of the ommatidium from outside. These pigmented cells also are modified ectoderm cells which lie between the adjacent ommatidial pits.

The morphological unit of the compound eye of *Serolis* may then be described as consisting of a group of ectodermic cells lying outside of the basement membrane, and so arranged as to form the walls of an open tubular depression. This group of cells undergoes special differentiations at different levels of the pit. The uppermost group, consisting of two flattened cells, constitutes the corneagen, which secretes the cornea externally; the second group of cells, consisting of two large cells, the vitrellae, secretes chitin towards the lumen of the tube, thus forming the crystalline cone; the third group of cells, the retinulae, consisting of four cells, secretes the rhabdomeres. The retinulae

are the only cells which are connected with the nerve centre. In addition to the three elements above named, the fourth element, in the form of two "hyaline cells," exists, plugging, as it were, from the inside the imperfect bottom of the depression. A number of pigment cells enveloping more or less completely the above mentioned group of cells from the outside constitutes the fifth element of the ommatidium.

A glance at the diagram (Fig. 1*b*, Pl. XXIX) will make this point clear. The diagram is supposed to be the plan of the constructive elements of the ommatidium of *Serolis* as they would appear when seen from the exterior, in the direction of the arrow, Fig. 1*a*, Pl. XXIX, if they actually formed an open pit like that shown in Fig. 2.

The innermost body which appears in the depression is the pair of "hyaline cells," (*d*); next above and therefore in the outer circle to (*d*) are.the retinulae (*c*), the rhabdomeres being represented by the yellow edges. Above the retinulae will come the two extremely enlarged cells, the vitrellae (*b*), whose chitin-secreting surface is marked by the yellow color. Next above (*b*) comes a pair of corneagen cells (*a*), whose chitin-secreting surface is also represented by the yellow color as in the cells forming the two inner series. The outermost of all is a pair of extremely flattened, pigmented cells, ensheathing completely the dioptric portion of the ommatidium.

The diagram is not unlike the one used in illustrating the arrangement of the different parts of a flower. This does not seem surprising when we remember that the nature of the problem in both cases is identical. Just as sepals, petals, stamens and pistils of a flower are considered as the modified leaves clustered round an extremely short stem or axis in whorls or in spirals, so the corneagen, vitrellae, retinulae, etc., are the modified ectoderm cells arranged at different heights on the ommatidial axis. There is, however, this difference between them, that while in a flower the parts concerned in the formation of the organ are themselves aggregations of many cells, those in the Arthropod ommatidium are highly differentiated individual cells; and while in the case of the flower it is the clustering of different parts around an extremely shortened projecting axis, in the ommatidium of the Arthropod it is the distribution of parts along an elongated and sunken one.

Although the subject will be much more intelligible after other types have been described, it will not be altogether out of place here to mention briefly my view of the steps through which the characteristic arrangement of parts in an ommatidium like that of *Serolis* might have been brought about. Suppose a circular area of the skin to be divided into five zones, one lying within the other. Mark the innermost circle as (1), and the next zone as (2), and the middle as (3), the fourth as (4) and the outermost as (5). Suppose, further, this circular area of the flat ectodermal surface of the body to sink down as a conical pit with its open base turned towards the exterior. The cell or cells lying in the innermost circle (1) in the middle of the area will sink deepest, while the outermost circle (5) will retain its original level. The cells lying in the innermost circle (1) are the "hyaline cells"; those lying within the second zone (2) are the retinulae; those lying in (3) are the vitrellae; those within (4) are the corneagen, and those within (5) are the group of pigmented cells which surround the dioptric portion of the ommatidium.

All that is necessary to convert this diagram into the ommatidium of *Serolis* is to reduce the lumen of the pit until it finally disappears and the cells facing the lumen of the tube come into contact with each other, or else remain separated by the chitinous structure; a faint line like that shown by x in Figs. 1, 3 and 4 being all that remains of the axial cavity, like that shown in Fig. 2.

The compound eye of *Serolis* is in this view nothing but a collection of these depressions in the skin, which by virtue of their aggregation attain the morphological and physiological value of an organ.

b. Talorchestia.

(Figs. 3, *3a*, Pl. XXIX.)

A glance at the figures will at once show the fundamental similarity of the ommatidium of this Amphipod and that of *Serolis*. Fig. 3, Pl. XXIX, shows a single ommatidium of *Talorchestia*. The outermost covering *c* is the corneal facet. The two cells which lie beneath it are the corneagen (*c. g*). These cells are not so conspicuous in the adult as in the young

animals; nevertheless, with care one can easily make them out. Beneath the corneagen comes the stratum consisting of two cells, the vitrellae, which secrete an enormous cuneiform, chitinous structure, the crystalline cone (*c. c*) with its more pointed end turned inward. The crystalline cone consists of halves, each corresponding to a single vitrella cell which secretes it on its median, axial surface. The line *x*, as in *Serolis*, shows the morphological lumen of the ommatidial cavity.

Next below this stratum comes the group of four cells, the retinulae (*Rt*). The chitinous edges of the retinulae meet in the median axis and form the rhabdom (*Rb*). Transverse striations, rather broad and coarse in their nature, are seen through the transparent cuticle, the rhabdomere. At the lower part of a retinula cell, near the basement membrane, is situated its nucleus (*n*); it may be found below the membrane.

The retinula cell undergoes a curious modification at the upper end. Each of the retinula cells sends out a flattened process which is highly pigmented and which completely ensheaths the dioptric portion of the ommatidium from the outside. In fact, the place of pigment cells (*pg. c*) in *Serolis* is taken by the modified upper expansion of the retinula cells. Outside of this pigmented sheath there exists a number of non-pigmented, elongated ectodermal cells (*p. c*) which pack the interspaces between the adjacent ommatidia.

If we plot out the whole structure into a diagram, in the same way as we did the ommatidia of *Serolis*, it will assume the appearance shown in Fig. 3*a*, Pl. XXIX. The innermost cells, the "hyaline cells" of *Serolis*, are not represented; the cells in the second circle are greatly developed (*Rt*), meeting one another with their chitin-secreting edges, the rhabdomeres, while the upper extremity of each retinula cell envelops the crystalline cone from the outside, thus physiologically taking the place of pigment cells, (*pg. c*) or 5 in *Serolis*, Fig. 1*b*, Pl. XXIX.

In the third circle the two vitrellae are found with their chitin-secreting surface marked yellow. The cells in the fourth circle constitute the corneagen (*c. g*). The fifth circle of cells is represented by the packing cells (*p. c*).

c. *Cambarus.*

(Fig. 4, Pl. XXIX; Fig. 35, Pl. XXXI; Figs. 71, 79, Pl. XXXV.)

In Fig. 4, Pl. XXIX, three ommatidia of *Cambarus* are represented, *a*, *b* and *c*. The ommatidium may be described as in the two preceding cases, as consisting of three strata of cells, each stratum characterized by the special chitinous product which it secretes. The outermost stratum of cells, the corneagen (*c.g*)[1] secretes a slightly biconvex corneal facet (*c*).

Next below the corneagen comes the stratum of vitrellae, consisting of four cells, each with an extremely elongated internal process. The median surface of the vitrella which corresponds to the chitin-secreting surface of the vitrella in *Serolis* and *Talorchestia* secretes a perfectly transparent, homogeneous substance, rather refractive in its nature, forming the crystalline cone (*c. c*). I cannot say anything of the chemical nature of this substance in its relation to the chitin. The cells which secrete this substance in the crayfish are morphologically identical with the vitrellae in *Serolis* and *Talorchestia* which secrete chitin, and the use this body subserves in the ommatidium of the crayfish is identical with that of the chitinous body, the crystalline cone, in the two Arthropods we have already examined. There can be no question of the homology of this body to the crystalline cone of other Arthropods. I have therefore represented this body in the yellow color as in *Serolis* and *Talorchestia*. The outline of the vitrella cell in the figure has been made diagramatic to a certain extent.

Next below the vitrellae come the retinulae, the whole being aggregated into a spindle-shaped bundle.[2] On the distal end of

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[1] Reichenbach (*Studien zur Entwicklungsgeschichte des Flusskrebses*, p. 93) speaks of these cells as "Semper'schen Zellen." In examining his figure (Fig. 225, Taf. XIV) we find what he regards as "Semper's cells," are those with "Semper'schen Kerne" (S. K.) The term "Semper's nucleus" as originally used by Claparède and adopted by others does not mean the nucleus of the corneagen, as Reichenbach uses it, but means that of the vitrella. In fact the existence of corneagen has been ignored by several earlier writers. It was Patten who emphasized its importance.

[2] This spindle stratum does not come from any part of the "augenfalte" of Reichenbach, but arises in the region where he locates the ectodermal and mesodermal pigment cells, *loc. cit.* Fig. 225, Taf. XIV.

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the rhabdom the proximal ends of the vitrellae apparently terminate.[1]

When the spindle is macerated and each of its component elements is examined individually, it is found that each retinula develops on its median surface a thick chitinous border which shows a wavy, corrugated appearance. This chitinous border attains its greatest thickness in the midst of the retinula cell (Fig. 35, Pl. XXXI). When the chitin-secreting edges of a number of these retinula cells meet they form a spindle-shaped bundle, the thickest part of the rhabdomere corresponding to the most bulging part of the spindle. The lower extremities of the retinula cells send out nerve processes, each of which forms an optic nerve fibre, (*Op. n*, Fig. 4, Pl. XXXI). Fine elongated cells filled with yellow pigment granules are found between the adjacent retinula bundles (*ep*, Fig. 4). They are also the modified ectodermal cells. The pigment cells which occur around the vitrellae form a complete envelope around the dioptric portion of each ommatidium.

Thus even with this complicated type of ommatidium the plan of structure is fundamentally alike to that of *Serolis*. The central element, the "hyaline cells" of *Serolis*, is not represented in the crayfish. To this special point I shall recur.

If we plot out the ommatidial elements of the crayfish as we did those of *Serolis*, exactly a similar kind of diagram will be formed. Thus in the centre will come the group of retinulae,

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[1] Parker found in *Homarus* (*A Preliminary Account of the Development and Histology of the Eyes in the Lobster*. Proceedings of the American Academy, Vol. XXIV, pp. 24–25, 1888) that the lower extremities of vitrellae run over the spindle, and that each terminates on the retinal side of the basement membrane. It is probable that the same is true in *Cambarus*. This fact is perfectly intelligible according to the view which is maintained in the present paper, for the cells found in the higher level of a given ommatidium are morphologically situated in the outside of those found in the lower. Patten's account (*Eyes of Molluscs and Arthropods*, Mittheilungen aus der Zoologischen Station zu Neapel, Bd. VI, Heft 4, 1886) that the rhabdom is the continuation of the retinophorae (vitrellae) is not true. I macerated the "spindle" of *Penaeus*, upon which Patten bases his observations, and found that it is composed of a number of pigmented retinula cells, each with its chitinous border as in *Cambarus* (Fig. 35, Pl. XXXI) or in *Homarus* (Fig. 34, Pl. XXXI). Grenacher is right in regarding the rhabdom as the secretion product of the retinula cells.

consisting of seven cells; then come in the outside four vitrellae arranged in a square; then two corneagen cells; and outermost of all, four pigmented cells which completely envelop the dioptric part of the ommatidium.

d. Homarus.

(Fig. 34, Pl. XXXI.)

The compound eye of *Homarus* has quite recently been studied by Parker.[1] I do not find any facts in Parker's paper which contradict the view maintained in the preceding pages in regard to the nature of the ommatidium. The threefold differentiation of the ectodermal cells in the walls of the ommatidium is just as evident here as in the forms already considered. The problematical body, the spindle (Grenacher's rhabdom), like the corresponding structure in *Cambarus*, resolves itself into a number of individual retinula cells with thick, serrated, chitinous secretions as in the case of *Cambarus* and *Penaeus*.

In Fig. 34, Pl. XXXI, four retinula cells are partly isolated from one another. The lower end of each retinula cell is prolonged into an optic nerve fibre, while the upper end is devoid of any pigment granules. A large translucent nucleus exists near the distal extremity of the retinula. The distal end of each cell is prolonged into a short, clearly defined, tapering process. The development of the chitinous serrature is greatest in the middle of the chitin-secreting border of the retinula; when, therefore, the whole is brought together into a bundle, the general outline of such a structure is spindle-shaped.

e. Callinectes.

(Figs. 5, 5*a*, Pl. XXIX; Fig. 37, Pl. XXXI; Fig. 72, Pl. XXXV.)

Callinectes presents the same interesting modification which we saw in *Talorchestia*. We find the corneagen cells and the vitrellae in two successive strata, but no special pigment cells embracing this dioptric mechanism exist. The packing cells which we saw in the intervening spaces of the ommatidia in *Talorchestia* are not found in *Callinectes*.

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[1] G. H. Parker: *A Preliminary Account of the Development and Histology of the Eyes in the Lobster.* Proc. Amer. Acad. Vol. XXIV, 1888.

The third stratum of cells, the retinulae, are extremely elongated, each retinula with a clear, straight, finely striated rhabdomere. A somewhat diagramatic representation of the individual retinula cell with its chitinous border is given in Fig. 37, Pl. XXXI. In Fig. 5*a*, Pl. XXIX, the upper portions of the two retinula cells are shown; the rhabdomere just beneath the crystalline cone shows a slight enlargement. The size of the retinula cell at the distal extremity undergoes an enlargement. The enlarged extremities of the retinulae form a pigmented collar around the inner end of the crystalline cone. If the upward extension of this part of the retinula cells be carried still further, a condition which prevails in a retinula like that of *Talorchestia* will be found. In the freshly teased preparation, one or more refractive globules, ranging from yellow to reddish brown in color, are found in the thickened portion of the retinula. The general shape of the ommatidium as determined by the shape of the corneal facet is hexagonal.

For the general discussion of the subject I do not find it necessary to go into further details of comparison, nor to enumerate more examples from different Arthropods. In the forms I have studied in this connection, representing near thirty Arthropod genera, I found nothing which invalidated the general interpretation of the ommatidial structure of the Arthropod as explained in the preceding pages, and the compound eye of the Arthropod, whether it be sessile or stalked, must be held to represent morphologically a group of ectodermal pits or a bundle of ectodermal tubules.

III.—The Compound (Lateral) Eye of Limulus.

The question which next suggests itself is this: Adopting for a moment the view that the ommatidium of the compound eye is morphologically an ectodermic pit, is there any adult arthropod whose eye permanently remains in this condition?

I find such an ommatidium in the compound eye of *Limulus*.

On this account I will describe the eyes of *Limulus* somewhat in detail.[1] In the succeeding section of the paper I will point

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[1] An outline of this portion of the paper will be found in the March number of the *University Circular*, 1889, Johns Hopkins University, under the title *The Structure and Development of the Eyes of the Limulus.*

out how an ommatidium like that of *Limulus* may be converted into one of a more complex type.

a. General Sketch of the Compound Eye.

The compound eye of *Limulus* is placed in the dorso-lateral angle of the prosomatic shield. In the fully grown animal the outline of the eye is bean-shaped, with its longer axis parallel to the longitudinal axis of the body. This bean-shaped area is slightly protuberant from the surrounding level; the chitinous covering of the body is thinner, softer, and more translucent in the region of the eye than on the rest of the dorsal surface. Through the translucent chitin we see a large number of circular spots, all of a uniform size. On further examination we find that each spot corresponds to a conical projection of the chitin, which fits into a cavity in the skin. This conical thickening of the chitin constitutes the *lens* or *lens-cone*, and the group of cells forming the walls and bottom of the open cavity constitute the essential part of the ommatidium.

The cells which form the walls of the pit are elongated and highly pigmented, forming the perineural cells (*p. n*, Fig. 6, Pl. XXIX); those cells which form the bottom of the pit undergo extreme enlargement compared with the perineural cells, and elongate along the longitudinal axis of the pit. They are grouped in a characteristic manner, reminding one of the arrangement of cells in the taste-bulb of a vertebrate. This bulb-like group of cells is the essential part of the retina. In my preliminary account of the subject[1] I called this group of cells an ommatidium. Properly speaking, the term ommatidium includes the whole group of cells forming the walls and bottom of the pit, together with the lens-cone and the thick chitinous covering corresponding to the area occupied by a single pit. In this latter sense the term ommatidium will be used in the present paper, and the bulb-like group of cells at the bottom of the pit will be designated as the *sensory part of the ommatidium*.

In the sensory part of the ommatidium, which consists of two portions, a central *a* and a peripheral *b*, the arrangement of the cells is quite regular.

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[1] *loc. cit.* p. 70.

The central part always consists of a single ganglion cell (*G*, Fig. 6, Pl. XXIX), and the peripheral of the rod-bearing pigmented cells (*Rt*, Fig. 6) which surround the former in the centre. As to the minute structure of these elements I shall speak later on. The cells composing the sensory portion of the ommatidium send out from their proximal ends nervous processes, which, forming a bundle, are seen to emanate from the basal end of the ommatidium. The number of nerve fibres at the beginning of the bundle and that of the cells composing the sensory bulb of the ommatidium always correspond. These bundles, however, soon break up as they penetrate deeper, and become mixed up with the fibres from the neighboring bundles, forming a complex plexus underneath the ommatidial area. Scattered in the plexus are found a number of thickenings, which, in gold-chloride preparations, appear as darkly stained masses of protoplasm occurring at the nodes of junction of the several intercrossing fibres (Figs. 44 and 45, Pl. XXXII). In the fresh state these enlargements contain a variable amount of yellow granules imbedded in the mass of the protoplasm. In the figures above referred to, mere outlines of such thickenings are given.

After the nerve fibres have formed the plexus they again come out in bundles, and piercing through the perforations in the basket-like chitinous support which underlies the ommatidial region, travel forward, slightly inward, then downward and backward until they terminate in the optic ganglion in the brain.

b. The Structure of the Ommatidium.

In the general sketch of the compound eye of *Limulus* above given, the structure of its morphological unit, the ommatidium, has been briefly described. It consists of two parts, (1) the sensory and (2) the dioptric part, which is also partly protective.

The sensory part consists of two factors, (*a*) the central element or the ganglion cell (*G*, Fig. 6, Pl. XXIX), and (*b*) the peripheral elements or the retinulae (*Rt*, Fig. 6). These two kinds of cells are the only ones in which nerve fibres terminate.

The retinula cells group themselves in the shape of a bulb, or something as the several segments do in an orange, each segment corresponding to a single rod-bearing cell or retinula (Fig. 10,

Rt, Pl. XXX). Along the axial side of the retinula cell there exists a definite longitudinal tract which is free from the pigment granules. On the outside of this colorless region there exists a thin layer of chitin. This chitinous covering on the outside of the retinula constitutes the rod or the rhabdomere (*Rb*, Fig. 10, Pl. XXX). When the non-pigmented portion of the retinula cell is examined with a high power, we find the whole structure to be transversely striated. This striated appearance seems to be produced by the existence of an enormous number of transverse fibrils lying in the inside of the chitinous cuticle. That these striae are due to the existence of independent fibrils is further shown by the fact that by careful focusing up and down of the microscope some striae can be directly traced out beyond the limit of the chitinous covering, in the form of independent fibrils (*Tr. fb*, Fig. 10, Pl. XXX).

When we make a transverse section of the retinulae, each cell will present a wedge-shaped outline, with its pointed end turned toward the axis of the ommatidium; the non-pigmented part of the cell in its relation to the cuticular secretion on the outside will be seen from the diagram (Fig. 6*a*, *b*, *Rb*, Pl. XXIX).

The number of retinula cells entering into a single ommatidium is quite variable. Thus, Grenacher[1] counts fifteen; Lankester and Bourne[2] count ten; I have found some with eleven, others with nine; in one ommatidium I counted as many as nineteen.

I am not able to say under what conditions this numerical variation takes place. Whatever significance there may exist in this numerical variation, it does not alter in the least, as in the case of different elements in other ommatidia we have already considered, the general idea that the ommatidium of the Arthropod is morphologically a depression in the skin.

Each ommatidium contains a single ganglion cell. Only in one case did I see two ganglion cells in a single ommatidium. The ganglion cell is situated morphologically in the centre of the sensory part of the ommatidium. The retinula cells completely envelop this ganglion cell from the outside, in a similar way as the rods encircle the cone in the centre in the retinae of some vertebrates.

[1] *loc. cit.* Fig. 125, Taf. XI.

[2] *loc. cit.* Fig. 10, Pl. XI.

The main body of the ganglion cell where the nucleus is situated is found in the lower part of the ommatidium, occupying in most cases an eccentric position. Figs. 13, 14 and 15, Pl. XXX, show three ganglion cells completely isolated from the rest of the retinal cells. In Fig. 10, Pl. XXX, the relation of the ganglion cell to the retinula cell is well shown.

The ganglion cell is distinguished by constant and well marked features from the rest of the ommatidial cells. The cell is bi-polar, the one process going upward and outward through the axial channel of the ommatidium (the axial canal of the rhabdom), and the other going downward and inward to the subommatidial plexus and thence to the brain. For the sake of convenience the former will be designated as the axial process (*Ax. p*, Figs. 13, 14, etc.), and the latter as the optic nerve process (*Op. n*, Figs. 13, 14, etc.) of the ganglion cell.

The axial process gradually tapers to a narrow point. The process consists of a bundle of extremely fine fibrils, which are distinctly seen as a series of longitudinal striae. For some mechanical causes, the distal process was seen split into three main branches in one specimen (Fig. 15, Pl. XXX); in another specimen (Fig. 10), the topmost end of the axial process was seen completely macerated into a number of component fibrils, the whole showing a brush-like appearance.

The large, translucent, spherical nucleus (*N*, Figs. 10, 13, 14, 15, Pl. XXX), with its nucleolus, is found in the substance of the cell body proper. The position of the nucleus is very often eccentric, as in Fig. 14. The nucleolus is surrounded by concentric markings in all cases. Between the nucleus and the proximal process there is always a larger or smaller patch of pigment granules (*Pg.p*, Figs. 10, 13, etc.). The color of the granules ranges from light yellow to dark brown or even to jet black. The yellow-colored pigment is diffused more or less widely through the body proper of the ganglion cell. Even in the same patch of pigment in the cell there are different gradations in the color. From the nature of the drawing used in the present paper I cannot show these gradations. Pigment patches may exist in other parts of the cell, but they never form so constant a characteristic as the group between the proximal process and the nucleus.

The third element which figures prominently around the sensory cells of the ommatidium is the eipithelial cell. The cell may either be pigmented or non-pigmented. In Fig. 11, Pl. XXX, a group of four retinula cells is shown partly isolated from one another. Within the interspaces between the adjacent retinula cells will be found a number of pigmented epithelial cells, extremely elongated, many of them extending the whole length of the retinula cell. In Fig. 12, Pl. XXX, a number of highly attenuated epithelial cells (*Ep*) is shown closely clinging to the outer surface of the retinula cell. In Figs. 10, 13, 14 and 17 highly attenuated epithelial cells (*Ep*), both of the pigmented and the non-pigmented kind, are shown, as they occur either around the ganglion cell or around the retinula cell.

In no case are these epithelial cells found to establish any organic connection with any part of the sensory cells or of their processes. These attenuated epithelial cells do not differ in any essential way from the ordinary ectodermal cells which are found in the walls of the ommatidium or in the general ectoderm.

The epithelial cells as they further depart from the periphery of the group of sensory cells, become stouter and thicker. One end of each epithelial cell is usually devoid of pigment granules; this non pigmented end of the cell secretes the chitin which forms the lens-cone. We have already seen that the portion which secretes the chitinous covering, the rhabdomere, of the retinula cell is devoid of pigment granules. In this respect the epithelial cells which form the wall of the pit and the neuro-epithelial cells which form the bottom of the pit closely agree with each other.

A glance at the series of figures (Figs. 17–33, Pl. XXXI) will show the degrees of modification undergone by the epithelial cells teased out from the different parts of the ommatidium. Those cells (Figs. 17 and 18) which lie at the bottom of the pit undergo the greatest modification. Fig. 17 is the central ganglion cell of the ommatidium, with a few slender epithelial cells around it. Fig. 18 is the retinula cell with a few pigmented epithelial cells clinging to its side. Both differ from the rest of the epithelial cells in their possession of nerve processes. In some epithelial cells, as in Figs. 28 and 25, Pl. XXXI, the degree of attenuation is so very great that the protoplasmic character of

the cell body is hardly recognizable. The cell body is represented by an extremely slender, bristle-like filament, with no pigment granules in the inside. In others this hyaline cell body is divided into a number of branches, as shown in Figs. 21 and 24, Pl. XXXI. In other ones, one-half of the cell body is reduced to a hyaline filament, while the other half retains a protoplasmic nature, with a greater or less amount of pigment granules as in Figs. 19, 20 and 24, Pl. XXXI; while in still others the protoplasmic substance is mostly gathered around the nuclei and the two extremities reduced to hyaline structures with no pigment granules in them, as in Figs. 22, 24, 27, 29 and 30, Pl. XXXI.

The contents of the ommatidium of *Limulus* may be put, then, under two categories: (1) the epithelial cells; (2) the products of secretion of these cells. The first may be classified into two principal divisions: (*a*) the neuro-epithelium, (*b*) the ordinary epithelium. The neuro-epithelium is of two kinds, the *central, ganglion cell* and the *peripheral, retinula cells.* The ordinary epithelium shows all varieties of modification, and exists either in the interspaces of the neuro-epithelium or around it. The products of secretion may also be put under two heads: (*a*) the chitin secreted by the neuro-epithelium (the retinula cells) forming the rhabdom; (*b*) the chitin secreted by the ordinary epithelium forming the lens-cone, and the entire chitinous structure lying over the pit.

The basement membrane (*B. M*, Fig. 6, Pl. XXIX) underlies the whole ommatidium, separating it completely from the underlying mesodermic tissue (*Ms*, Fig. 6, Pl. XXIX). At the bottom of the ommatidium the basement membrane follows the course of nerve fibres issuing from the bases of the neuro-epithelial cells, and thus forms a complete sac to the bundle of nerve fibres. When the bundle breaks up in the plexus the basement membrane sheath of the optic nerve fibres becomes indistinct.

A study of transverse sections of the ommatidium at different heights will show the relative positions of the component elements a little more clearly. In Fig. 6*a*, Pl. XXIX, transverse sections of the ommatidium cut at four different levels are shown, and will be intelligible if one compares them with Fig. 6, Pl. XXIX.

In (*a*) Fig. 6*a*, the plane of section passes near the opening of the pit. In the centre is found a portion of the lens (*L*), and

surrounding it a circular row of columnar pigmented epithelium. The lens is secreted by the surrounding columnar cells. Around the whole ommatidium there exists a rather thick, well defined basement membrane (*B. M*) which separates the ommatidium from the mesodermic tissues (*Ms*).

In (*b*) Fig. 6*a*, a section at about the level of the letters *Rt*, in Fig. 6, passing through the sensory portion is shown. The main contents of the ommatidial capsule (*B. M*) are the retinula cells (*Rt*). The axial moiety of each retinula cell is free from the pigment granules, and a thin cuticular covering is secreted around this portion of the cell. This cuticular covering constitutes the rhabdomere (*Rb*). Sections of a number of pigmented cells are seen lying between the retinulae and the basement membrane; these are sections of the perineural epithelial cells.

In (*c*), Fig. 6*a*, a section passing through the body of the ganglion cell (*G*) is shown; the ganglion cell is surrounded by a circle of retinula cells, which are now gradually tapering, each into a slender nerve process. The ganglion cell takes a more eccentric position in (*d*) than in (*c*). The retinula cells (*Rt*) in (*c*) and (*d*) are represented by the circle of nerve fibres surrounding the ganglion cell (*G*).

In (*e*), Fig. 6*a*, the section passes through the bottom of the ommatidium; all of the sensory cells are reduced into nerve fibres which proceed one from the bottom of each cell. The basement membrane (*B. M*) is still distinctly seen, forming the sheath of the nerve bundle. The interspaces of the adjacent ommatidia are occupied by the mesodermic connective tissue.

If we plot out the arrangement of the component elements in the ommatidium of *Limulus*, the appearance shown in Fig. 7 will be presented. The epithelial cells (*Ep*) forming the walls of the pit are drawn with their chitin-secreting surfaces turned towards the axis of the ommatidium, which is morphologically the exterior surface of the body.

c. The Development of the Compound Eye.

The first rudiments of the compound eye appear extremely early in the embryonic stage as a pair of ectodermal thickenings above the level of the "dorsal organ." In Fig. 39, Pl. XXXII, * shows the place where the compound eye makes its

appearance. In this stage the "dorsal organ" (*D. O*) is already very prominent. The eye itself does not show its characteristic invagination, but is represented by a slightly thickened patch of the ectoderm; except in the microscopic examination of the sections it is hardly recognizable. The section Fig. 42, Pl. XXXII, shows an embryo considerably more advanced than Fig. 39. The plane of section passes obliquely forward from behind, and cuts both the eye (*E*) and the "dorsal organ" (*D. O*). The most noticeable feature in this stage of the development of the eye is the existence of the lateral invaginations at the edges of the ocular area. The section shows three portions, the dorsal fold (*d. f*) and ventral fold (*v. f*), with the median portion (*E*) between them. The groove along which the ectoderm invaginates is V-shaped, with the pointed end turned towards the posterior end of the body. As the invagination becomes deeper, the pointed end of the V becomes prolonged into a tube, which works its way beneath the general surface of the ectoderm. This tubular invagination of the posterior part of the eye will be called the median fold of involution (*m. f*) in our subsequent descriptions.

The whole outline of the invaginated area may be represented by Y, the area intercepted by the two divergent branches of the Y being the ommatidial portion, while the posterior stem of the Y is the continuation of the lateral depressions, the median fold, extending backward and downward beneath the surface of the general ectoderm.

The opening of the tube is at the junction of the two divergent branches of the Y with the posterior median stem.

Figs. 47–56, Pl. XXXIII, represent a series of transverse sections of the compound eye in the stage represented by Fig. 42, Pl. XXXII. Fig. 47 is the section passing through the anterior end of the ocular area. The ectodermic cells are considerably thicker than the general ectoderm in this region. The section which comes immediately behind this is not given in the plate. Fig. 48 shows essential characters of the section which immediately follows the section Fig. 47. At two portions of the thickened ectoderm, *d. f* and *v. f*, the cells arrange themselves in radial fashion, accompanied by a characteristic change in each nucleus, which becomes coarsely granular and peculiarly translucent.

In examining the next section, Fig. 49, the radial arrangement of cells in the above section is shown to be the beginning of invagination. In Fig. 49 the lateral invaginations *d. f* and *v. f* have each a well developed lumen. In the median side the walls of the invaginations become continuous with the group of finely divided cells, each with darkly stained nucleus. This group of cells give rise to ommatidia. The outer wall of each invagination becomes continuous with the columnal epithelial covering of the body.

Figs. 50 and 51 show essentially the same thing. The ommatidial area (*Om*) in Fig. 51 becomes wider than in any of the preceding sections.

Just at the point where the maximum width of the ommatidial area is reached (Fig. 51), it again begins to become narrow, for in the section (Fig. 52) which comes immediately behind that shown in (Fig. 51), the ommatidial area is narrower compared with that shown in Fig. 51, and the two lateral folds of invaginations approach each other, resulting in a fusion in the median line in Fig. 53. In Fig. 54 the fused lateral folds, resulting in the formation of the median fold (*m. f*), begins to work its way beneath the level of the skin. In Fig. 55 a few cells (*m. f*), forming the posterior extremity of the median fold beneath the skin, are found. The section (Fig. 56) passing behind that shown in Fig. 55 shows no trace of invagination of any kind.

The anterior end of the eye, then, begins with Fig. 47; two sections behind it a beginning of lateral invaginations becomes discernible; at Fig. 53 the two lateral folds fuse, and at the ninth section (Fig. 54) they form a median tube (*m. f*), and at Fig. 56 the posterior boundary of the ommatidial area terminates.

In Figs. 45*a* and 46*a* are shown the longitudinal sections of the eye. The ommatidial cells in the anterior portion of the eye send out nerve fibres which form the optic nerve (*Op. n*). The basement membrane (*B. M*) which underlies the ectodermal cells forms a complete sheath to the bundle of optic nerve fibres going to the optic ganglia of the brain, which are formed by independent involutions on the ventral side of the body.[1] The origin

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[1] The optic ganglia arise as ectodermic involutions in the pre-oral region of the animal. Owing to the existence of a great cephalic flexure in *Limulus*, that side where the optic ganglia as well as the median eye originate has for the sake of convenience been called the "ventral side."

of the optic nerve fibres is further shown in Fig. 43, Pl. XXXII. The figure shows an oblique transverse section through the ommatidial region of a more advanced embryo than the one shown in Fig. 45*a*, Pl. XXXIII. The plane of section passes through the ommatidial area and through the bundle of the optic nerves, which run forward. The migration of the ectodermal cells seems to take place from the periphery to the inside of the body. The basement membrane (*B. M*) forms a continuous sheath around this migratory stream of ectodermal cells.

In Fig. 40, Pl. XXXII, is shown an embryo in the so-called "trilobite stage." A pair of round protuberant organs (*D. O*) in front of the eyes (*E*) are the "dorsal organs." The eye is distinctly marked in this stage, owing to the formation of pigment granules in the component cells. Except in the general enlargement of the organ and the formation of the pigment granules in the cells, the eye in this stage does not offer any material difference from the condition seen in the stage which we have already examined (Figs. 47–56). After the first moult of the chitinous covering from the condition represented in Fig. 40, Pl. XXXII, it passes into a more advanced condition when the essential Limuloid features characteristic of the adult become distinctly discernible. Fig. 41, Pl. XXXII, represents the young *Limulus* at its first stage in the acquisition of the external Limuloid features. The whole body is translucent; the chitinous covering of the body is yet extremely thin, and the dendritic ramifications of the "liver" containing the remnant of the food-yolk of various hues, sometimes green, at other times yellow or pink, shine through the transparent tissues of the body.

The compound eye (*E*) shows an interesting feature in connection with the formation of the ommatidial area.

Figs. 57–64, Pl. XXXIV, show a series of transverse sections through the compound eye in the stage shown in Fig. 41, Pl. XXXII.

Fig. 57, Pl. XXXIV, represents a section passing through the anterior part of the eye. The ectoderm in the ommatidial area is thrown into a number of folds. The cells lying in the valley of the fold are destined to give rise to the ommatidium. In the dorsal margin of the ommatidial area there exists a thick layer of ectoderm, consisting of a number of large cells, each with

granular protoplasm and a large nucleus. At the basal end of each cell there exists an accumulation of transparent liquid substance. Beneath ommatidial area a well defined basement membrane (*B. M*), which is the continuation of the same membrane existing under the general ectoderm of the body, sharply marks out the ommatidial structure from the mesodermic tissues.

In Fig. 58, which is taken a few sections behind the preceding, is shown the ommatidial area at its widest part. Four ommatidia formed by the undulating folds of the ectoderm are shown, each depression being accompanied by a corresponding thickening of the chitin, forming the rudiment of the lens-cone (*C*).

On both sides of the ommatidial area we find the lateral invagination of the ectoderm. The cells forming the invaginated folds undergo enormous enlargement, and in the basal end of each cell is shown a large accumulation of transparent fluid. The cells forming the inner walls of the dorsal and ventral folds of invaginations undergo various metamorphoses. Each of them becomes divided into a number of smaller cells, each of these segments being packed with extremely fine pigment granules. As the cells in the inner walls of the dorsal and ventral folds (*d.f*, *v.f*) become divided up into a number of smaller pigmented segments, they are constantly pushed out towards the surface, where they, grouping themselves into a number of ommatidia, increase the general surface of the ommatidial area. Thus, the older ommatidia are found in the middle and the younger ommatidia are to be found around the marginal portion of the ocular area.

In Fig. 59 a section is shown in which the ommatidial area is narrower than the preceding. In Figs. 60 and 61 this narrowing of the ommatidial portion continues, and in Fig. 62 the dorsal and the ventral folds meet in the median line. In Fig. 63 the median fold becomes completely buried beneath the general ectoderm. In Fig. 64 the section passes near the posterior extremity of the median fold, where the reduction in the size of the tube as well as its increased distance from the level of the general ectoderm is clearly discernible.

In all the figures above described *Pg. c* means the pigment cells, which in the state of nature are highly pigmented, each with a small eccentric nucleus. Each section has been carefully

depigmented, without which the process of the formation of the ommatidia and the increase of the ocular area is perfectly unintelligible. Those cells in the figures which have no granular structure are, in the state of nature, charged with a large quantity of pigment granules, and those large cells forming the walls of the lateral folds are granular and free from pigment granules.

Transverse sections are not fitted for the study of the formation of the nerve fibres. In this stage, as in the preceding ones, each ommatidium sends out nerve fibres from its basal end towards the interior of the body. Besides the cells in the bottom of each ommatidial pit, each gigantic cell of the outer walls of the dorsal and ventral folds sends out a nerve process from its basal end, which runs inward and forward, joins the nerve fibres from the bottom of each ommatidium, forming a large bundle, and goes to the brain.

The invagination of the lateral and posterior margin of the ocular area is usually not permanent. With a growth of the animal and an increase of the surface of the ocular area, the invaginated folds, both on the sides as well as behind the ocular area, become stretched out in the adult animals and leave no trace of their existence. Occasionally, however, one meets in the adult with a remnant of the involuted tube in the posterior part of the eye, which exists as a ball of pigment cells buried in the midst of the mesodermic tissue.

The history of the ommatidial cells in the compound eye of *Limulus* may then be stated in the following way:

(1). A stage of undifferentiated ectodermal cells.

(2). Thickening of these undifferentiated cells, accompanied with the invagination beneath the surface.

(3). Extreme enlargement of the invaginated ectoderm, followed by the acquisition of pigment granules and by division.

(4). Pushing out of the resulting small pigmented cells towards the surface where they differentiated into two fundamental groups: (*a*) Ordinary epithelial cells, which secrete the chitinous cuticle over the ocular area, including the lens, or pack the interspaces of the neuro-epithelium; (*b*) neuro-epithelium, consisting of the rod-bearing retinulae and the central ganglion cells, the two forming the sensory portion of the ommatidium.

IV.—PHYLOGENY OF THE OMMATIDIUM.

I do not pretend to enter into a detailed discussion of this difficult problem. In order, however, to give a more intelligent idea of what I have thus far been considering, I will devote the following pages to the reconsideration of facts given in the preceding pages from a more comprehensive standpoint.

Balfour[1] has given a sketch of the possible evolution of a visual organ. He starts with a simple organism in which a spot on the surface of the body may become spontaneously pigmented and therefore become specially sensitive to light. The cuticular covering of the body may become thickened at this spot and act as an apparatus for condensing the light upon the pigmented spot lying beneath it. He further expresses his view elsewhere[2] that the lens-like dioptric apparatus of the eye, formed either as a thickening of the cuticle or as a mass of cells, was at first formed simply to concentrate the light on the sensitive spot; the power to throw an image of external objects on the perceptive part of the eye was acquired gradually afterward.

The part which is played by pigment in the physiology of vision is considered a most obscure problem. I quote the following, clearly put forward by Foster,[3] as a physiological aspect of the question bearing upon the discussion at issue: "But in order that light may produce chemical effects (upon protoplasm), it must be absorbed; it must be spent in doing the chemical work. Accordingly, the first step towards the formation of an organ of vision is the differentiation of a portion of protoplasm into a pigment at once capable of absorbing light and sensitive to light—*i. e.* undergoing decomposition upon exposure to light. An organism, a portion of whose protoplasm had thus become differentiated into such a pigment, would be able to react towards light. The light falling on the organism would be in part absorbed by the pigment, and the rays thus absorbed would produce a chemical action and set free chemical

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[1] F. M. Balfour: Address to the Department of Anatomy and Physiology, British Association, 1880; *Nature*, Vol. XXII, p. 417, 1880.

[2] *Comparative Embryology*, Vol. II, Chapter XVI, Organs of Vision, p. 470.

[3] M. Foster: *A Text Book of Physiology*, 4th Edition, Book III, Chap. II: Sight; The Photochemistry of Retina, pp. 515–516.

substances which before were not present. We have only to suppose that the chemical substances are of such a nature as to act as a stimulus to the protoplasm of other parts of the organism (and we have manifold evidence of the exquisite sensitiveness of protoplasm in general to chemical stimuli), in order to see how rays of light falling on the organism might excite movements in it, or modify movements which were being carried on, or might otherwise affect the organism in whole or in part. Such considerations as the foregoing may be applied to even the complex organ of vision of the higher animals. If we suppose that the actual terminations of the optic nerve are surrounded by substances sensitive to light, then it becomes easy to imagine how light, falling on these sensitive substances, should set free chemical bodies possessed of the property of acting as stimuli to the actual nerve-endings, and thus give rise to visual impulses in the optic fibres."

Lubbock[1] advances essentially the same idea as Balfour's in his recent work on the subject, illustrated with some lucid diagrams. "In the simple forms," he says, "the whole surface is more or less sensitive. Suppose, however, some solid and opaque particles of pigment deposited in certain cells of the skin. Their opacity would arrest and absorb the light, thus increasing its effect, while their solidity would enhance the effect of external stimulus. A further step might be a depression in the skin at this point, which would serve somewhat to protect these differentiated and more sensitive cells, while the deeper this depression the greater would be the protection."

That such steps of gradual development of visual organs have actually taken place in some forms is quite probable. In Arthropods, it seems to me worthy of remark that the ommatidium of the lateral eye of *Limulus* makes the nearest approach to this primitive condition. It is nothing more and nothing less than a depression in the skin, with the thickened chitinous cuticle fitting in the open cavity and acting as a lens to condense the light. The cells which form the sensory part of the structure are modified ectodermic cells, and, like the rest of the ectodermic cells lying on the surface of the body, secrete the chitinous cuticle on

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[1] *On the Senses, Instinct, and Intelligence of Animals*, Inter. Scie. Series, Vol. LXIX, 1888.

a part of their surface. Assuming the surface where the chitin is secreted to be the exterior, we may describe the ommatidium of the lateral eye of *Limulus* as a group of modified ectodermic cells aggregated around and beneath the funnel-shaped depression in the skin. A glance at the diagrams (Fig. 6, Pl. XXIX; Figs. 65 and 66, Pl. XXXV) will show this clearly. The sensory cells of the ommatidium come into direct contact with the conical lens, which is the thickened part of the general cuticle; or, to express this in the phraseology of Lankester and Bourne, the ommatidium in the lateral eye of *Limulus* is "epistatic." The cornea and crystalline cone as such have no separate existence in this stage.

Suppose such an ommatidium to become duplicated until a considerable number be formed, as we may safely imagine to have been the case, from the general tendency in the perfection of a visual organ. What will be the result? The first effect of such an increase of the number of ommatidia in a given area will be the lengthening of each unit in the direction of the ommatidial axis, and the cells (*V*, Fig. 67, Pl. XXXV) which were situated directly on the outside of the retinulae will travel over and above the sensory portion (*Rt* and *G*, Fig. 67). The distal ends of such cells (*V*) which were thus pushed over will meet one another in the median or the "optic axis" of the ommatidium; further, they will continue to secrete chitin (*c. c*, Fig. 67) from their original chitin-secreting surfaces which are now median and axial. The chitin thus secreted will have an independent existence from the cornea, thus forming the rudiment of the crystalline cone, and the cells themselves will form the vitrellae (*V*, Figs. 67, 68, etc.). Finally, as the deepening still further goes on, the corneal lens (*C*) and crystalline cone (*c. c*) will be entirely separated, thus producing a condition somewhat similar to that which obtains in *Serolis* (Figs. 69 and 70.)

From this point onward, the three chitinous structures, *cornea*, *crystalline cone*, and *rhabdomere*, undergo a different development in different Arthropods. In some the crystalline cone assumes a transparent semi-liquid state, while the whole cell becomes extremely elongated, forming the crystalline cone of certain crustacea (Fig. 71, Pl. XXXV); it may form a hard

chitinous ball as in *Serolis* (Fig. 70, Pl. XXXV); or a cuneiform chitinous structure, as in *Talorchestia* (Fig. 73, Pl. XXXV); or finally the whole cell may remain as a clear, transparent body, as in several insects, forming Grenacher's "aconous type" of the compound eye.

The forms assumed by the rhabdomeres in different Arthropods are equally diverse. The rhabdomere may exist as a plain cuticular covering over the non-pigmented part of the retinula, as in *Limulus* or in *Serolis* (Fig. 10, *Rb*, Pl. XXIX; Fig. 38, *Rb*, Pl. XXXI, etc.); it may become extremely elongated and narrow as in *Musca* or in *Callinectes* (Fig. 5, *Rb*, Pl. XXIX; Fig. 37, *Rb*, Pl. XXXI; Fig. 72, *Rb*, Pl. XXXV); it may become transversely folded as in *Cambarus* (Fig. 35, *Rb*, Pl. XXXI; Fig. 4, *Rb*, Pl. XXIX; Fig. 71, *Rb*, Pl. XXXV); these transverse folds may become still finer, showing the chitinous serrature along the axial edge of the retinula, as in *Penaeus* and *Homarus* (Fig. 34, *Rb*, Pl. XXXI); or this transverse serrature may become extremely fine and regular, as in *Squilla* (Fig. 36, Pl. XXXI).

The cornea undergoes equally diverse modifications according as it is purely protective, or partly protective and partly dioptric in function. The range of variation is shown by the degrees of curvatures and by the varieties of its thickness. In several of the decapod crustacea which I have examined, as *Penaeus*, *Cambarus*, *Homarus*, *Callinectes*, *Gebia*, etc., the curvatures of the individual cornea on both surfaces are very slight; it is biconvex in an extremely small degree. In *Talorchestia* both surfaces of the cornea are parallel. In *Serolis*, four species of which I have studied, all having well developed compound eyes, there exists a considerable difference in different species in the nature of the cornea. In some the curvature on the proximal surface is very strong and the whole structure is quite thick, while in others the cornea is rather thin and a slight development of curvatures exists. This is interesting, showing that even within the group of nearly allied species there are considerable differences in this respect.

This fact is easy to understand when we remember the functional property of the cornea and the crystalline cone. As has been noticed already, the crystalline cone is always dioptric in

function, while the cornea may be partly protective and partly dioptric, or wholly protective. When the cornea becomes partly dioptric, as in *Serolis* and in several other Arthropods, the dioptric function in an individual ommatidium comes to be performed by two structures, the crystalline cone and the corneal lens. When the two structures act together for the same end at the same time, it is easy to see how a certain trivial peculiarity of the one may induce a correlative modification of the other, and how a slight specific peculiarity may appear exaggerated in the thickness or in the degree of curvature of the corneal lenses in different species.

After so much has been said in regard to the unity of structure of the ommatidium in different Arthropods, one important point awaits our consideration, viz. the homology and fate of the central ganglion cell found in the ommatidium of *Limulus.* Unless a great many forms of ommatidia in different Arthropods be compared, a discussion on this point appears to be unprofitable. The consideration which follows is therefore a purely provisional one.

There can be no question that the central ganglion cell is an important factor in the ommatidium of *Limulus*, nor can we doubt the existence of a fundamental homology between the retinulae of *Limulus* and those of all the other Arthropods which I have examined. With the exception of a few problematical bodies, such as the "hyaline cells" of *Serolis*, there are no structures in the ommatidia of most Arthropods which correspond to the central ganglion cell of *Limulus*, in spite of the existence of a fundamental homology in the other elements of the ommatidium.

What has become of the central ganglionic element of the ommatidium? Was it lost in the course of the phylogenetic history of a more complex ommatidium? Or is it reasonable to suppose that some ommatidia came into existence without it from the beginning? Or, if it were lost at all, is there any evidence which makes this supposition probable?

The colorless ganglionic cell and the pigmented rod-bearing cells which surround the former I consider as the two primitive morphological factors in the unit of the sensory part of the Arthropod retina, somewhat in the same way as the circle of

rods with a cone in the centre are the two essential factors in the neuro-epithelial layer of the human retina. In the absence of enough comparative data in Arthropods at present we have to dwell largely on the analogy suggested in the other groups of animals. Whatever be the views as to the fundamental homology of the ommatidium of *Limulus* to a structural unit of the sensory part of the human retina, a superficial resemblance of the one to the other is certainly very strong. The structural resemblance is paralleled by a physiological one. The place where the light acts in the visual end-organ of Arthropods and of man may alike be considered as consisting of a number of definite groups of cells, each group being a morphological and a physiological unit; or, in other words, the sensory part of the retinæ in both cases consists of a mosaic of several sensitive spots. The image formed on such a surface is therefore a mosaic one, whether in an Arthropod or in a Vertebrate.

Fundamental as this arrangement appears to be in the human retina, these two factors are liable to variation in their relative distribution in different Vertebrates. In fact, the variation takes place between the two extremes where the rods alone exist on one hand and where the cones alone constitute the essential part of the retina on the other. Thus, according to Schultze, "either form of percipient element (rod and cone) may be represented by the other" in the Vertebrate. This range of variability in the distribution of the cones and rods occurs even in a single group of Vertebrates, as in mammalia, showing that the variation in the distribution of the essential factors, even within a tolerably well circumscribed group of animals, is sometimes quite extensive. The group of Arthropods is a heterogeneous one, and I see no *à priori* objection to believing in the existence of a phenomenon analogous to what we find in Vertebrates, viz. that the two percipient elements represented by the central and the peripheral cells in the ommatidium of *Limulus* may be differently represented in different Arthropods.

There is no doubt whatever that the retinula cells are homologous throughout the Arthropods. In fact, in most Arthropods which I have examined no other elements but the retinulae have any connection with the optic nerve fibres, and they often undergo an enormous development and acquire most complicated

structures, as in *Homarus* or in *Penaeus*, giving rise to the much discussed "spindle."

But what has become of the central element which is so conspicuous in the ommatidium of *Limulus*, if the retinulae in all Arthropods are homologous? I believe the central cell is fully functional, judging from its position and from its veritable connection with optic nerve fibre in *Limulus*. What in other Arthropods strongly reminds one of this cell is the "hyaline cell" at the bottom of the ommatidial pit in *Serolis* and, according to Beddard, also in the *Cymothoidae*. One important difference, however, exists between the "hyaline cell" of the Isopods and the central cell in the ommatidium of *Limulus*, viz. that, while in the latter the cell is connected with the optic nerve, the "hyaline cell" in the former has no connection with the central nervous system whatever. Hence the "hyaline cell" cannot be sensory, even if it be homologous with the central cell of *Limulus*, which it resembles in its general appearance and in its position. The number of "hyaline cells" in *Serolis* is always two, while its supposed homologue in *Limulus* is, as a general rule, only one. This fact does not offer any objection to my view of their homology, when we bear in mind that other elements in different ommatidia, as vitrellae and retinulae, show a wide range of variation so far as their numbers are concerned, and yet they can be considered as perfectly homologous.

A further embryological and comparative knowledge in regard to the "hyaline cell" in Isopods is necessary for the determination of its exact homology. Meanwhile I would observe that if the central and the peripheral cells which we see in the ommatidium of *Limulus* may be taken as the two essential factors of the sensory element of the typical Arthropod retina, the case of *Serolis* may be taken as a loss of balance in the relative development of these two factors; the central cells having lost their sensory function and remaining as a sort of supporting mechanism. We can imagine this change in the function of the central cell as carried still further, and with the excessive development of the peripheral elements, the retinulae, the central element may finally have disappeared.

All this is, however, a mere suggestion, and my interpretation of the nature of the Arthropod ommatidium in general does not

lose its force even if this section of my views in regard to the fate and homology of the central cell or cells be proved untenable. It is quite possible that the ommatidia in which there is no element corresponding to the central cell of *Limulus* may have originated without it from the beginning. It seems, however, more natural to suppose that such an ommatidium had it originally and lost it later, observing that the simplest form of ommatidium possesses it in its fully functional, sensory form.

Finally we have to consider the nature of the compound eye as a whole as presented in various types of Arthropods.

That a certain structure in the body of an animal may repeat itself and give rise to a secondary aggregate, or to a compound organ, is a well known fact; the repetition of similarly constructed uriniferous tubules forms the essential part of a vertebrate kidney, or the similar repetition of gill-filaments forms the respiratory organ of a Lamellibranch. Sundry other examples of this nature might be given, but the above two will suffice. Tracing, as I have attempted to do, the most complicated ommatidium into a simple, open ectodermic pit, there is to my mind no difficulty in believing that the compound eye of the Arthropod is one of the most astonishing examples of the formation of an organ by the vegetative repetition of the similar structure. Thus, according to Lubbock, there are about 4000 facets in the compound eye of the house-fly (*Musca*), each facet corresponding to a single tubular invagination of the skin, the ommatidium. There are 4000 independent invaginations in the area in the head of the fly occupied by the compound eye; in the gadfly (*Œstrus*) 7000; in the goat-moth (*Cossus*) 11,000; in the death's-head moth (*Sphinx atropos*) 12,000; in a butterfly (*Papillio*) 17,000; in a dragon fly (*Æschna*) 20,000; in a small beetle (*Mordella*) as many as 25,000. On the other hand, the number of ommatidia seems to have reached its minimum in certain Copepods, as in *Corycæus*, where the whole visual organ seems to be represented by a single colossal ommatidium.

Certain forms of Collembola[1] seem to have a very small num-

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[1] Lubbock. *Monograph of the Collembola and Thysanura*, the Ray Society, 1873, p. 57, Pls. LV and LVI. Lubbock uses the term "ocellus" to designate a single element of the eye which I here called an ommatidium. If the structure of this "ocellus" differs from the ommatidium of other Arthropods, it has, of course, nothing to do with the discussion at issue.

ber of ommatidia; thus in *Templetonia* only one ommatidium exists on each side of the head; *Orchesella* has six on each side of the head; *Tomocerus*, *Isopoma*, have seven; *Degeeria*, *Lepidocyrtus*, *Smynthurus* and *Papirius*, eight. In the ants we observe a similar gradation in the number of ommatidia.

What reasons can we assign for this enormous multiplication of similarly constructed parts? What advantage follows from this arrangement? If the view of the nature of the compound eye which is put forward in the preceding pages be a true one, Müller's celebrated theory of mosaic vision is the only one that can account for the enormous multiplication of the similarly formed pits in the skin. The subject has been so fully discussed by Lubbock that I need not enter into details here. "According to his (Johannes Müller's) view, those rays of light only which pass directly through the crystaliine cones, or are reflected from their sides, reach the corresponding nerve fibre. The others fall on and are absorbed by the pigment which separates the different facets. Hence each cone receives light only from a very small portion of the field of vision, and the rays so received are collected into one spot of light. *The larger and more convex, therefore, is the eye, the wider will be its field of vision; while the smaller and more numerous are the facets, the more distinct will the vision be.* In fact, the picture perceived by the insects will be mosaic, in which the number of points will correspond with the number of facets."[1] The whole explanation of the problem seems to me to be contained in the passage above cited; and no further comment will be necessary more than a statement that the increase in the number of ommatidia is a decided advantage to their possessor. An eye like that of *Limulus* might by a slight change be converted into one of a more protuberant nature so as to command a wider field of vision, as we see in some species of *Serolis* or in some Trilobites; a slight change again might produce a protuberant ocular area mounted on an ophthalamic stalk, and accompanied by the accessory apparatus of vision, such as the socket for protection or the set of muscles to move the eye-stalk in different directions so as to command a still wider field of vision. In this connection I may refer to a series of diagrams (Figs. 74–81, Pl. XXXV). The black heavy layer repre-

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[1] Lubbock: *Senses, Instinct and Intelligence*, p. 163.

sents the ectoderm, and the region in which the ectoderm is thrown into folds the area of the compound eye. The yellow colored layer outside represents the chitin, and the dotted line beneath the ectoderm, the basement membrane.

In *Limulus* (Fig. 74) the ectoderm is thrown into a series of shallow folds, which, when viewed from above, would be a group of shallow pits in the skin. Each pit is an ommatidium. In *Serolis* (Fig. 75) the invagination of the skin is a little deeper than that of *Limulus*, and the whole ocular area is more prominent. Fig. 76 represents the condition of the ectodermal folding in *Notonecta*, and Fig. 77 that of *Agrion* larva. Fig. 78 represents the eye of *Branchipus*, only a part of the stalk being shown in the figure. Fig. 79 represents the eye of *Cambarus;* Fig. 80 that of *Penaeus*, and Fig. 81 that of *Lucifer.*

It must not be understood that the number of folds given in the diagrams have anything to do with the actual number of ommatidia that may exist in the actual specimens; no more than a morphological expression of the eye in a simplest possible form was intended. If one suppose a single invagination of the skin, say of Fig. 79, be divided into three strata and the cells in the bottom stratum to send out nerve fibres, those in the middle to form the crystalline cone and those in the outermost to form the cornea (Fig. 71), the interpretation of the diagram will be complete.

According to this view the compound eyes of Arthropods, either in the sessile or in the stalked form, are nothing more than a collection of ectodermic pits whose outer open ends face towards the sources of light, and whose inner ends are connected with the central nervous system by the optic nerve fibres. The cells forming the walls of the pit arrange themselves into three strata, in most cases accompanied by three regional functional differentiations. Grenacher's classification of the compound eyes of insects into "acone," "pseudocone" and "eucone" types refers to the condition of the cells and their products in the middle stratum—the vitrellae.

Morphologically, then, the compound eye of an Arthropod is strictly single-layered, although, as is evident, the present conception is entirely different from the monostichous theory maintained by some recent writers. From *Limulus* to *Squilla* we

have a series of forms showing all degrees of modification in the general structure of the eye as well as the structure of its individual elements, and there is not here a single form which invalidates the view maintained in the present paper. Moreover, this view has the advantage of greatly simplifying our conception of these structures, reducing, as it does, all of them to one primitive structure, a depression in the skin, in which several organs of ectodermal nature, often of a very complicated type, find their common morphological origin. And when thus the nature of the unit is reduced into a simple invagination of the skin, the formation of the compound eye appears to be but another instance of the well known method in the formation of a morphological organ, namely, *the vegetative repetition of a similar structure.*

V.—Summary.

In studying the structure of the ommatidium of the compound eye of *Serolis* it has been found that it may be reduced to a simple ectodermic invagination of the skin. Extending my researches over several other Arthropods, of which *Talorchestia*, *Cambarus*, *Homarus*, and *Callinectes* were mentioned in the preceding pages, the same interpretation of the ommatidium may be applied without exception. This view of the ommatidium finds its strongest support in the fact that in *Limulus*, the ommatidium is an open pit of the skin.

By supposing that the ommatidial pit of *Limulus* became deeper and that this was accompanied by modifications in the structure and arrangement of the component cells, we can show the probability of our first supposition that the ommatidium of the compound eye of an Arthropod is an independent invagination of the skin. If this view is correct, the unit of the compound eye of an Arthropod is not, after all, so complex a structure as has been supposed by some; and the enormous increase in the number of ommatidia in a given area of the skin which results in the formation of the compound eye finds its parallel in the well known method of the formation of morphological organs, viz. the duplication of a simple unit.

Baltimore, *April* 30, 1889.

VI.—Appendix.

The Compound Eye of Echinoderms.

While the preceding paper on the compound eye of Arthropods was passing through the press I improved my opportunity to study the compound eye of Echinoderms at Woods Holl, during the months of June and July, 1889, to see how far the morphological interpretation advanced for the former will hold to the latter.

The three starfishes common at Woods Holl, viz. *Asterias vulgaris*, Stimp., *Asterias forbesii*, Verril, and *Cribella sanguinolenta*, Lutken, were studied in this connection. While I reserve the description of the details for a future paper, I will briefly point out some important bearings of the results upon the subject which has been discussed in the preceding pages.

The general structure of the compound eye of the starfish at the tip of each ray is well known through the writings of Hæckel, Wilson, Hoffmann, Lange, Greeff, Hamann, Carrière, and some others, although there exist some discrepancies in regard to the histological features of the organ as described by these naturalists.

The most remarkable observation on the eye of the Echinoderm among the early writers is that of Goodsir, who, according to Forbes,[1] is said to have examined the eye of *Cribella oculata* and remarked of its structure that it consisted "*of a red cushion with pits on its surface.*" My studies on the compound eyes of the starfishes convinced me of the truth of Goodsir's statement, and the eye of a starfish is nothing more than a group of ectodermal conical pits with their bases turned towards the exterior. The epithelial cells which form the walls of the conical pit have each a cuticular rod secreted at the tip of its distal extremity.

These cells send out nerve fibres from their proximal extremities. In the centre of the pit along the longitudinal axis of the invagination there is a space filled with a clear fluid substance. The cuticular secretions of the retinal cells, as well as the colorless fluid substance, constitute together a translucent

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[1] E. Forbes: *A History of British Starfishes, and other Animals of the class Echinodermata.* London, 1841, p. 102.

refractive body in the centre of each pit or the ommatidium, which has been described by several as the "crystalline cone" in the starfish eye. The whole surface of the eye-bulb is covered by a thin cuticle which is secreted by the cells whose distal extremities lie on the general level of the external surface of the optic bulb. In short, this external cuticular covering of the eye in a starfish corresponds to the *cornea*, and the cuticular secretions at the distal extremities of the retinal cells forming the walls of the pit, correspond to the *crystalline cone* and the *rhabdom* of the compound eye of an Arthropod. The colorless fluid substance contained in the axial space of the invagination in the starfish may be compared to the similar substance in the crystalline cone of the ommatidium of *Serolis*. The number of ommatidia in the starfish increases at the periphery of the optic tract as in an Arthropod. The spaces between the adjacent ommatidial invaginations are occupied by the supporting epithelial cells. The optic nerve fibres pass into the deepest stratum of the epithelial layer, and running horizontally, join the main branch of the ventral nerve cord of the ray.

On the whole, the entire morphological arrangement of the parts in the compound eye of an Echinoderm is strikingly similar to that of an Arthropod, and the formation of the visual organ in the Echinoderms, at least in one of the large sub-groups, the *Asteridæ*, by a series of ectodermic invaginations, assumes a wider significance when we take into consideration the fact that the compound eye of the Arthropods has a similar mode of origin, although it is an independent adaptation.

In the anatomical consideration of the Echinoderm eye I have made no allusion to the so-called "eye-spot" on the ocular plate of the sea-urchin. In regard to the function of this structure we are by no means certain that it is visual in nature as it is usually assumed. Valentin failed to discover any trace of dioptric apparatus in it. More recently Fredericq[1] could not find any evidence, anatomically and experimentally, that the structure in question is an eye. "*La tache de pigment qu'on y décrit est une pure fiction.*"

[1] Fredericq, Léon: *Contributions à l'étude des Echinides.* Archives des Zoologie Experi. et Gener., Tome 5, 1876, p. 434.

Hamann,[1] who studied this structure in Echinus, declares that the so-called "eye-spot" in the sea-urchin bears a close resemblance to the terminal feeler at the tip of arm of a starfish, with which he thinks it is homologous and not with the eye. He therefore substitutes the term "intergenital plate" for the "ocular plate" upon which this problematical organ rests.

Even if this organ be shown to have some connection with the visual function, as Romanes and Ewart[2] claim on the ground of their experiments, it is safe to say that it belongs to a different category of visual organ, as Hamann's histological study clearly shows, and has nothing to do with the subject under our consideration, viz. the morphology of the *compound eye* of the Echinoderm and the Arthropod.

Entirely apart from the preceding, but which may be mentioned in this connection, is the Sarasins' discovery[3] of the compound eyes in a sea-urchin (*Diadema*) from Ceylon. Of their visual nature there can be no doubt, as their experiments on the living animals as well as the anatomical structure of the eyelet show.

The eyelet of the compound eye in *Diadema* is very much more complex than that of the starfishes I have examined. I cannot help but believe that a study of development of such an interesting form as *Diadema*, as well as a more extensive study of the eye in different genera and species of Echinoderms, will throw a great deal of light on the morphology of the compound eye in general.

In my main paper on the subject I hope to describe in detail the structure and development of the compound eye of the starfish that I have studied, and also to give an account of the growth of our knowledge of the visual organ of the Echinoderms, both anatomical and experimental, from Tiedman and Ehrenberg down to the present day.

[1] Hamann, Otto: *Beiträge zur Histologie der Echinodermen.* Jenaische Zeitschrift für Naturwissenschaft, Bd. 21, 1887, pp. 124–126.

[2] Romanes, J. G., and Ewart, J. C.: *Observations on the Locomotor System of Echinodermata.* Philosophical Transactions, Royal Society, London. Pt. III, 1881, pp. 855–856.

[3] Sarasin, P. B. and C. F.: *Ueber einen mit Zusammengesetzten Augen bedeckten Seeigel.* Zoologischer Anzeiger, 8 Jahrg. No. 211, 1885. Their main paper I have not seen.

VII.—EXPLANATION OF FIGURES.

List of Reference Letters.

Ap. Appendage.
Ax.p. Axial process of the ganglion cell.
B. M. Basement membrane.
C. Corneal lens.
c. Cornea or corneal facet.
c.c. Crystalline cone.
Ch. Chitin.
c.g. Corneagen.
d.f. Dorsal fold.
D.O. Dorsal organ.
E. Eye (compound).
Ect. Ectoderm.
Ent. Entosternite.
Ep. Epithelial cell.
F.y. Food-yolk.
G. Ganglion cell.
H. Hyaline cell.
L. Lens-cone.
Ms. Mesoderm.
N. Nucleus.
Oc. Ocellus.
Om. Ommatidium.
Op.n. Optic nerve fibre.
p.c. Packing cell.
p.n. Perineural cell.
Pg.c. Pigment cell.
Pg.p. Pigment patch.
Rb. Rhabdomere.
Rt. Retinula.
Tr.fb. Transverse striae.
V. Vitrella.
V.C. Ventral nerve chain.
v.f. Ventral fold.
x. Axial space or line of the ommatidium, corresponding to the cavity of the invagination.

PLATE XXIX.—*Serolis, Talorchestia, Cambarus, Callinectes* and *Limulus.*

FIG. 1.—*Serolis.* Two ommatidia of *Serolis;* the one on the left with the pigment cells enveloping the crystalline cone. The downward extensions of the rhabdomeres reach to the retinal side of the basement membrane. ½ (E × 2) Zeiss.

FIG. 1*a.*—*Serolis.* Diagram of the Ommatidium—

a. Corneagen.
b. Vitrella.
c. Retinula.
d. Hyaline cell.
1. Cornea.
2. Crystalline cone.
3. Rhabdomere.
Pg. c. Pigment cell.

FIG. 1*b.*—*Serolis.* Plan of the Ommatidium—

1. Hyaline cell (*d*).
2. Retinula (*c*).
3. Vitrella (*b*).
4. Corneagen (*a*).
5. Pigment cell (*pg. c*).

FIG. 2.—Morphological diagram of the ommatidium of *Serolis*—

a. Corneagen.
b. Vitrella.
c. Retinula.
d. Hyaline cell.
1. Cornea.
2. Crystalline cone.
3. Rhabdomere.

FIG. 3.—*Talorchestia.* Ommatidium of *Talorchestia.*—*Rt'*, upward extension of the retinula *Rt*; this upward extension sometimes reaches as far as the cornea. *p. c.* Narrow, non-pigmented packing cells. ½ (D × 4) Z.

FIG. 3*a.*—*Talorchestia.* Plan of the Ommatidia.

FIG. 4. *Cambarus.* Three ommatidia shown side by side. In *c* the pigment cells (*pg. c*) completely envelop the crystalline cone. *x* is the morphological lumen of the invagination. *Ep* is the epithelial cell charged with light yellow pigment granules. ½ (D × 2) Z.

FIG. 5. *Callinectes.* Two ommatidia shown side by side. Rhabdomere (*Rb*) shows a fine striation. At the swollen end of the retinula (*Rt*) yellow or brown colored globules are found.

FIG. 5*a.*—*Callinectes.* Head of the retinulae more highly magnified, and the rhabdomeres show slight enlargement at the terminal portion.

FIG. 6.—*Limulus.* Two ommatidia shown side by side, partly schematic. The thick yellow-colored body is the chitinous covering of the eye. *L.* lens-cone, fitting into the depression of the skin. At the bottom of the depression, the essential part of the ommatidium

is found, consisting of two parts, *Rt* (retinulae) and *G* (central ganglion cell). Cells forming the walls of the pit are the perineural cells (*p. n*). Inward prolongations of the neuro-epithelial cells (*Rt* and *G*) form the optic fibres (*Op. n*). *Ms.* Mesodermic tissue.

FIG. 6*a*.—*Limulus.* Transverse sections of five ommatidia at different levels. In (*a*) the plane of section passes through the upper part of the depression, cutting the lens-cone (*L*); in (*b*) the section plane passes through the retinulae, showing the star-shaped rhabdom and the axial process of the ganglion cell (*Ax.p*) in the axial canal of the rhabdom. A few pigmented perineural cells surround the retinulae, while the basement membrane (*B. M*) forms the complete capsule of the ommatidium, separating the latter from the mesodermic tissue (*Ms*). In (*c*) the plane of section passes through the lower part of the ommatidium, cutting the central ganglion cell (*G*); in (*d*) the ganglion cell occupies an eccentric position; in (*e*) the sections of optic nerve fibres alone are seen.

FIG. 7.—*Limulus.* Plan of the ommatidium. *Ep* represent the cells which are found in the walls of the pit; the yellow edge corresponds to the surface where the chitin is secreted.

PLATE XXX.—*Limulus.*

FIG. 10. Retinula (*Rt*) and ganglion cell (*G*) teased out from the ommatidium after treatment with Haller's fluid 15 hours. The axial process (*Ax. p*) of the ganglion cell closely follows the external border of the rhabdomere (*Rb*). A number of epithelial cells are found closely attached to the surface of the retinula as well as to the ganglion cell. $\frac{2}{3}$ (E × 2) Z.

FIG. 11. A bunch of retinulae completely isolated from the ommatidium. Pigmented epithelial cells (*Ep*) are found between them. The proximal ends of retinulae form the optic nerve fibres (*Op. n*). $\frac{2}{3}$ (E × 2) Z.

FIG. 12. A retinula cell seen from the side opposite to the rhabdomere. A number of extremely attenuated epithelial cells (*Ep*) are found closely clinging to the external surface of the cell. They do not form any connection with the retinula, and can be completely isolated from it. The cell-body of such an elongated epithelium is reduced to a very slender filament and does not contain any pigment granules. $\frac{2}{3}$ (E × 2) Z.

FIG. 13. The central ganglion cell with its axial process (*Ax. p*) completely isolated. The pigment patch (*Pg. p*), situated between

the nucleus (*N*) and the optic nerve fibre (*Op. n*), shows a characteristic mark of the cell. A zone around the nucleus (*N*) shows concentric markings. Longitudinal striae run through the axial process and the optic nerve; (*Ep*) an attenuated epithelial cell. $\frac{2}{3}$ (E × 2) Z.

Fig. 14. Another type of the central ganglion cell. Pigment patch is greatly extended; nucleus (*N*) is eccentric; (*Ep*) attenuated epithelial cells. $\frac{2}{3}$ (E × 2) Z.

Fig. 15. The central ganglion cell, with its axial process (*Ax. p*) divided into several branches, by some mechanical causes. All these branches are longitudinally striated like the main one and would seem to be made up of a collection of extremely fine longitudinal fibrils. Two pieces of chitinous body (*Rb*) are found at the junction of the axial process and the cell-body proper of the ganglion cell. They appear to be fragments of the rhabdomeres. $\frac{2}{3}$ (E × 2) Z.

The specimens figured in Figs. 10–14 were treated with Haller's macerating fluid; that shown in Fig. 15 was treated with sulphuric acid, 8 drops to 30 grams of water.

Fig. 16. Epithelial cells isolated from the margin of the ommatidial depression. The part in which there is no pigment is turned outward and comes in direct apposition to the chitin.

Plate XXXI.—*Limulus, Homarus, Cambarus, Squilla, Callinectes, Serolis.*

Figs. 17–33.—*Limulus.* This series of specimens is intended to show the range of modification of the epithelial cells found in the ommatidium and its direct neighborhood.

Fig. 17. Central ganglion cell with several attenuated, non-pigmented epithelial cells. $\frac{2}{3}$ (E × 2) Z.

Fig. 18. Retinula cell with a few pigmented epithelial cells at its side. $\frac{2}{3}$ (E × 2) Z.

Figs. 19–33. Ordinary epithelial cells isolated from the ommatidial region. $\frac{2}{3}$ (E × 2) Z.

Fig. 34.—*Homarus.* Retinulae partly isolated. Each retinula secretes a chitinous body which assumes a serrated appearance (*Rb*). This is the rhabdomere; when the bundle is brought together it assumes a spindle shape. The upper part of each retinula cell is free from pigment, and is connected with the pigmented portion by a long, slender neck. The nucleus of the retinula is situated at the non-pigmented, distal extremity. $\frac{2}{3}$ (D × 2) Z.

Fig. 35.—*Cambarus.* The retinula completely isolated. The rhabdomere shows a coarse wavy outline. $\frac{2}{3}$ (D × 2) Z.

Fig. 36.—*Squilla*, partly diagramatic.

Fig. 37.—*Callinectes*, partly diagramatic.

Fig. 38.—*Serolis*, partly diagramatic.

The last three figures are introduced here so as to show the homology of the retinula cells in different groups of Arthropods.

All the specimens figured in this plate were treated and macerated in Haller's fluid.

Plate XXXII.—*Limulus.*

Fig. 39. Young embryo of *Limulus.* *D. O.* "Dorsal organ"; * shows the position where the compound eye makes its appearance.

Fig. 40. Larval *Limulus* in the so-called "trilobite stage"; immediately after hatching. *D. O.* "Dorsal organ"; *E.* Compound eye; *Oc.* Ocelli.

Fig. 41. Young *Limulus* at the first stage in the acquisition of the external Limuloid characters. The whole body is transparent and the dendritic ramifications of the "liver" shining through the transparent tissues of the body. The "dorsal organ" has completely disappeared in this stage. *E.* the compound eye; and *Oc.* Ocelli.

Fig. 42. Transverse section of a young larva, showing the origin of the compound eye (*E*), the formation of the dorsal and ventral folds of invagination (*d.f* and *v.f*), and the "dorsal organ" *D. O.* $\frac{2}{3}$ (A × 2) Z.

Fig. 43. Transverse section of the compound eye, showing the formation of the optic nerve fibres by the migration of the ectodermal cells. $\frac{2}{3}$ (D × 4) Z.

Fig. 44. Outline of the thickening of the nerve plexus beneath the ommatidial layer. $\frac{2}{3}$ (E × 2) Z.

IG. 45. The same. $\frac{2}{3}$ (D × 4) Z.

Both are drawn from the gold-chloride preparations.

Fig. 46. Ganglionic swelling found in the optic nerve fibres of the median eye. $\frac{2}{3}$ (4 × D) Z.

Plate XXXIII.—*Limulus.*

Fig. 45*a*. Longitudinal section of the eye, showing the formation of the optic nerve fibres (*Op. n*).

Fig. 46*a*. Oblique longitudinal section of the eye, showing the formation of the optic nerve fibres (*Op. n*).

FIGS. 47–56. Consecutive series of transverse sections of the compound eye of *Limulus* at the beginning of the lateral invaginations. Fig. 47, No. 1; Fig. 48, No. 3; (the section No. 2 is essentially the same as No. 3). Fig. 49, No. 4; Fig. 50, No. 5; Fig. 51, No. 6; Fig. 52, No. 7; Fig. 53, No. 8; Fig. 54, No. 9; Fig. 55, No. 10; Fig. 56, No. 11. The lateral invaginations become distinctly marked at Fig. 49, No. 4, and fuse in the median line at Fig. 54, No. 9, forming the median fold (*m.f*).

PLATE XXXIV.—*Limulus.*

FIGS. 57–64 show the condition of the lateral and median invaginations of the compound eye in the stage shown in Fig. 41, Pl. XXXII.

FIG. 57. In this the plane of section passes through the anterior part of the eye, and the dorsal invagination (*d.f*) of the compound eye is distinctly shown. The skin is thrown into folds; into the concave lumen of the fold a slightly thickened portion of the cuticle fits, forming the rudiment of the lens-cone (*C*); and the cells forming the walls of the invaginated fold form the beginning of the ommatidium.

FIG. 58 shows the widest portion of the eye in this stage; the beginning of the ventral invagination (*v.f*) is distinctly recognizable. The dorsal fold (*d.f*) is very large. Four distinct ommatidia are formed in this section, each depression being accompanied by a slight thickening of the corresponding portion of the cuticle (*C*). The basement membrane is very distinctly seen underneath the ocular area and beneath the general ectoderm cells which lie outside of the ocular area. The action of acid to which the sections were subjected in order to remove the pigment granules has interfered with the preservation of the ectodermal cells in those regions, although the thick, refractive basement membrane remains quite distinctly.

FIGS. 59, 60 and 61 show how the lateral invaginations are gradually approaching as we go towards the posterior part of the eye. In Fig. 62 the dorsal and ventral folds (*d.f* and *v.f*) meet in the median line, and in Fig. 63 they form a complete tube, the granular, non-pigmented layer coming to the outside and the pigmented cell layer (*Pg.c*) occupying the deeper part of the tube. The basement membrane (*B. M*) forms a complete capsule around the tube. The basement membrane which underlies the general ectoderm comes to

the outside of the median fold (*m.f*). Counting from the outside we meet with three consecutive strata of basement membrane in this region of the eye.

FIG. 64. In this we come nearly to the posterior extremity of the median fold (*m.f*). The median fold is further from the surface basement membrane than in Fig. 63.

PLATE XXXV.

FIGS. 65–69. Diagrams showing the probable evolution of the three-layered ommatidium from the single-layered surface depression in the skin, by the gradual subsidence of the neuro-epithelial elements, *Rt* and *G*, Fig. 65. In Fig. 66 the ommatidium of *Limulus* is represented, which is considered a step further advanced from the condition shown in Fig. 65. The distal end of the retinula (*Rt*) instead of being pointed toward the exterior as in Fig. 65, in *Limulus* it points towards the median axis of the ommatidium. The chitinous substance being still secreted on the outside, a distinct body of chitin beneath the lens-cone (*C*) is formed, the rhabdom (*Rb*). In Fig. 67 this deepening is supposed to have gone still further, resulting in the formation of another independent chitinous body, the crystalline cone (*C.c*). In Fig. 68 this deepening is considered to have advanced still further, the crystalline cone (*C.c*) being entirely separated from the corneal lens (*C*) by a distinct stratum of cell, the corneagen (*c.g*). In Fig. 69 an ommatidium with three strata of cells, each secreting chitinous substance on the part of their surface, is formed. These three strata of cells are known as the *corneagen* (*c.g*), the *vitrella* (*V*), and the *retinula* (*Rt*). Three chitinous bodies secreted by each group of cells above mentioned are the *cornea* (*C*), the *crystalline cone* (*c.c*), and the *rhabdomere* (*Rb*), respectively.

FIG. 70.—*Serolis.* Diagram of the ommatidium of *Serolis.* General arrangement of cells in this is not very different from that shown in Fig. 69. The place of ganglion cell in Fig. 69, *G*, is taken by a pair (of which only one is shown in the diagram) of transparent "hyaline cells" (*H*).

FIG. 71.—*Cambarus.* This is introduced in comparison with the hypothetical ommatidia.

FIG. 72.—*Callinectes.*

FIG. 73.—*Talorchestia.*

In the last three forms no element corresponding to the central

ganglion cell of *Limulus* nor to the "hyaline cell" of *Serolis* can be found. The sensory element of the ommatidium is represented by the retinulae (*Rt*) only.

FIG. 74.—*Limulus*. Diagram of the compound eye of *Limulus*, the black, heavy line representing the ectoderm and each depression in this layer corresponding to an ommatidium.

FIG. 75.—*Serolis*. In the same way as the above, the eye of *Serolis* may be represented by a series of folds.

FIG. 76.—*Notonecta.*

FIG. 77.—*Agrion* (Larva).

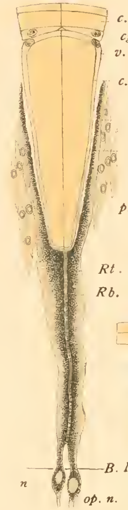
FIG. 78.—*Branchipus.*

FIG. 79.—*Cambarus.*

FIG. 80.—*Penaeus.*

FIG. 81.—*Lucifer.*

Fig. 3.



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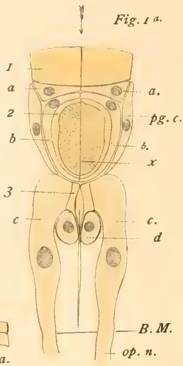


Fig.

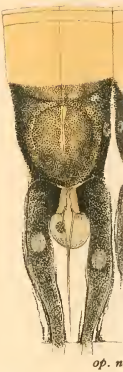


Fig. 2

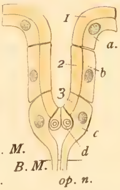
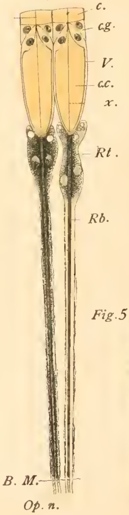


Fig. 5



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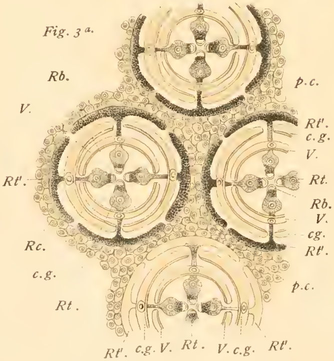


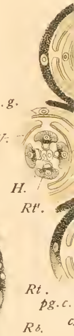


Fig. 5 a.

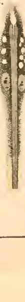


Fig. 4.

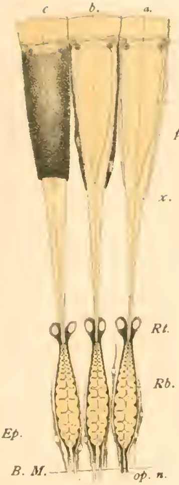
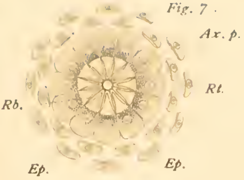


Fig. 7.



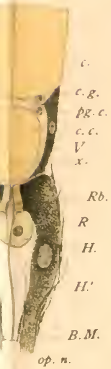
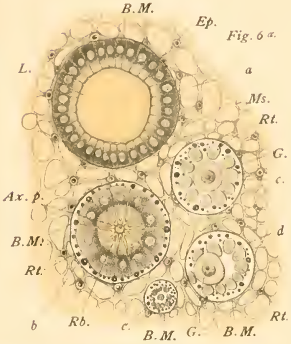
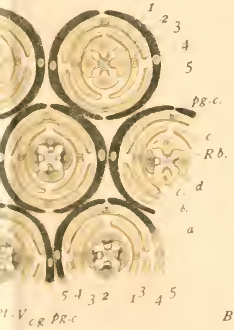


Fig. 1b.

Fig. 6a.





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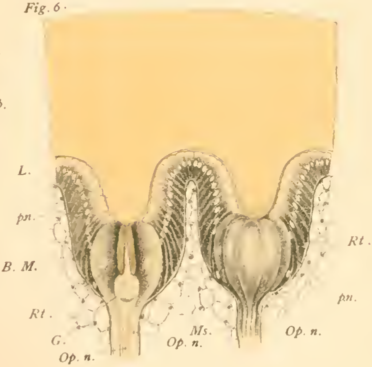

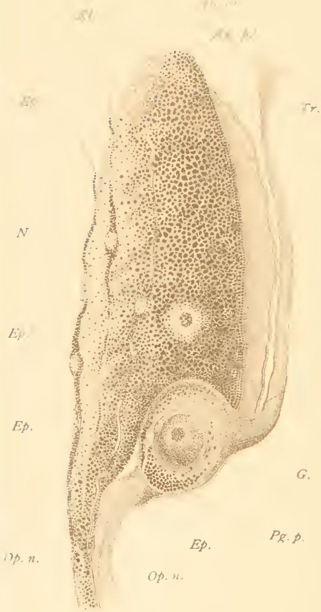

Rt.
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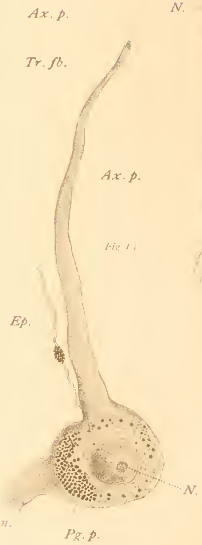
Ep.
Tr. fb.
Rb.
N
Ep.
Ep.
G.
Pg. p.
Ep.
Op. n.
Op. n.



Ax. p.
Tr. fb.
Ax. p.
Ep.
N.
Op. n.
Pg. p.

Fig 13

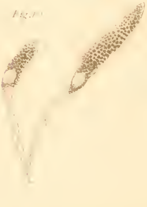


Fig. 1[illegible]

Rt.
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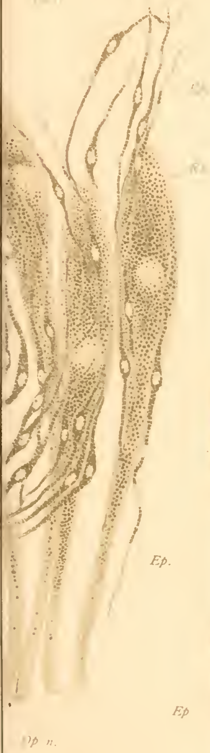
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Ep.
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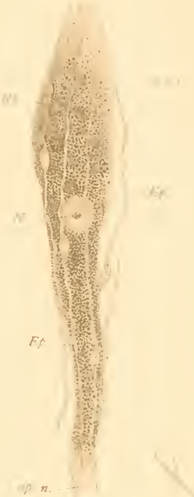
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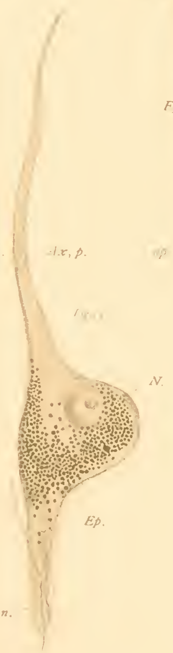
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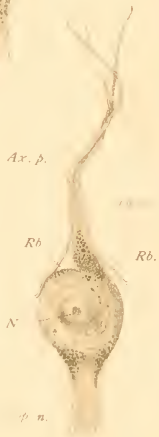
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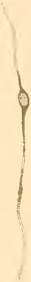

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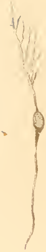
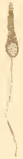


Fig. [illegible]

Fig. 2



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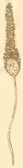

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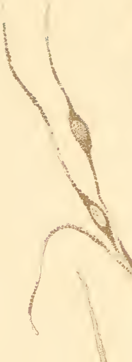

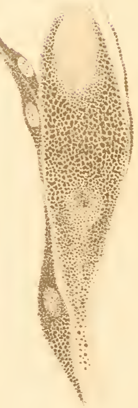

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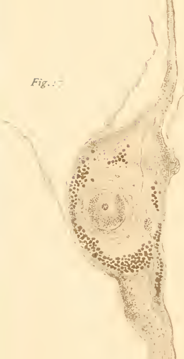

Fig. 17

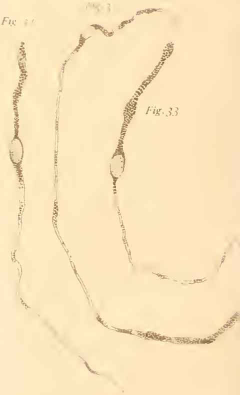

Fig. [illegible]

Fig. [illegible]

Fig. 33

Fig. [illegible]

Fig. [illegible]

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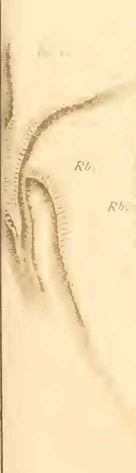

Fig. [illegible]

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Fig. [illegible]

Fig. 45

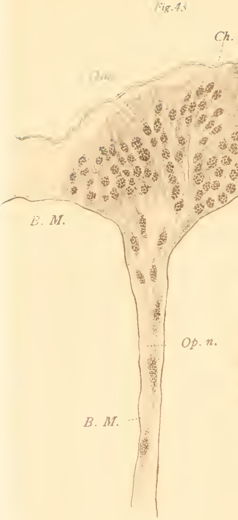


Fig. 39

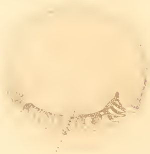
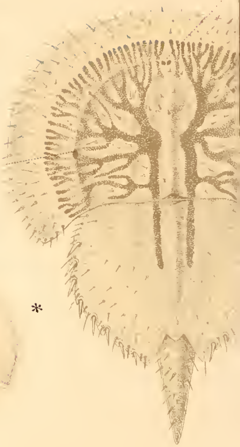
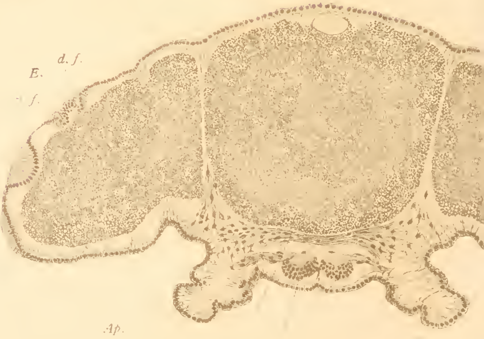
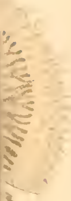
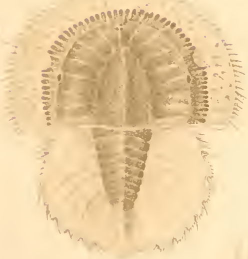


Fig. 11






E.


Oc.
D. O.
E
D. O.

E
D. O.

Fig. 44
Fig. 45

Fig. 47

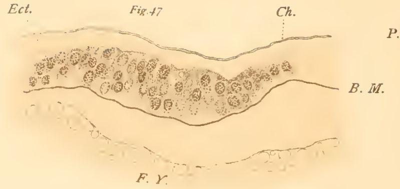


Fig. 48

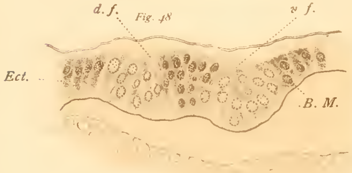


Fig. 49

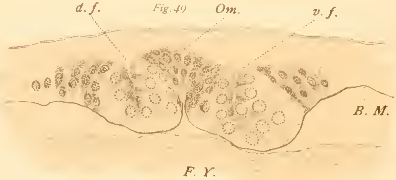
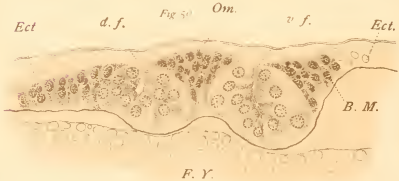
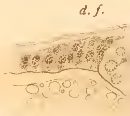
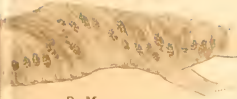


Fig. 50







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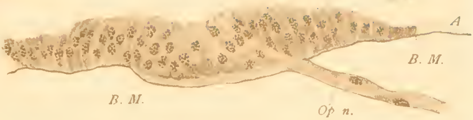


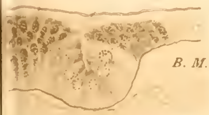


Fig. 54

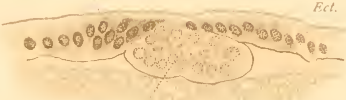


Fig. 51

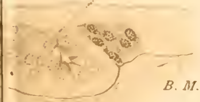


Fig. 55

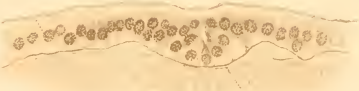


Fig. 52

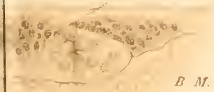


Fig. 56

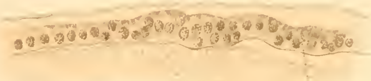


Fig. 57

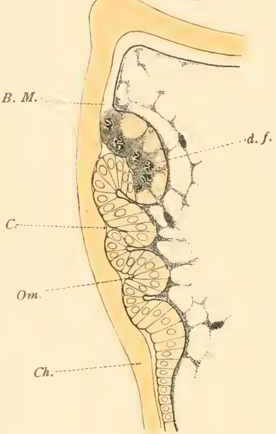
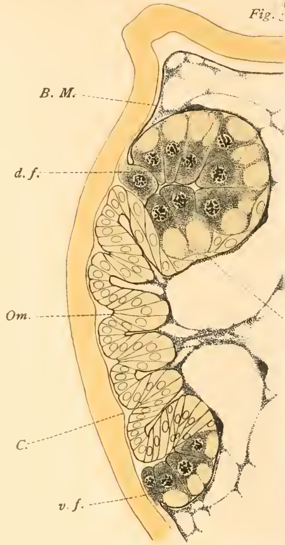


Fig.



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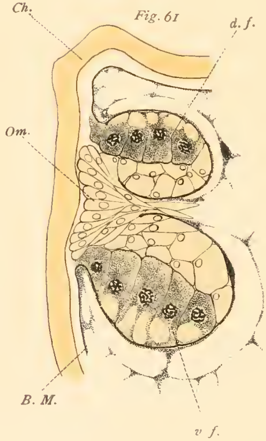

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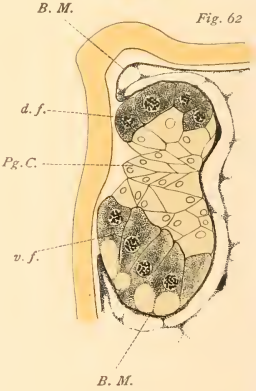

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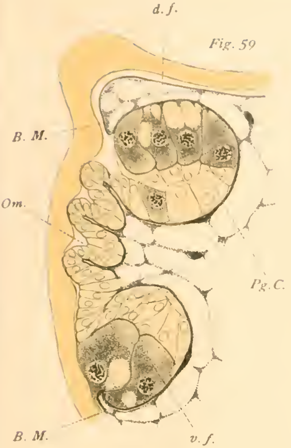

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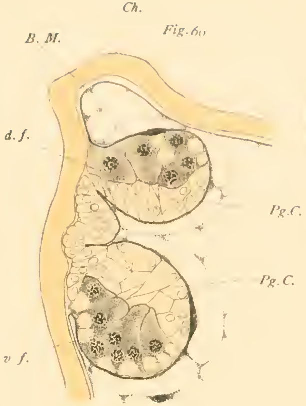

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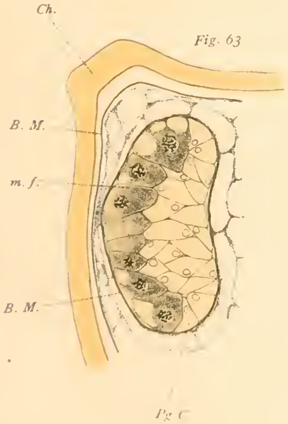

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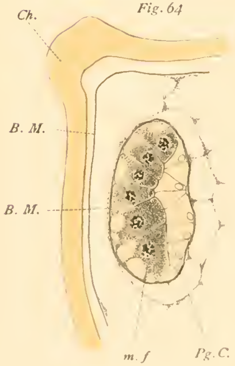

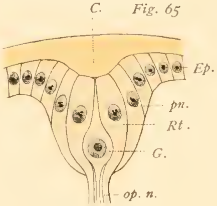

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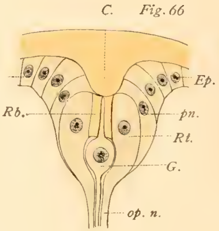
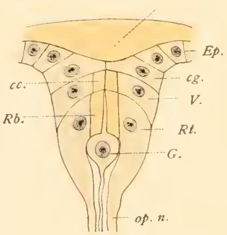


Fig. 66

Fig. 68



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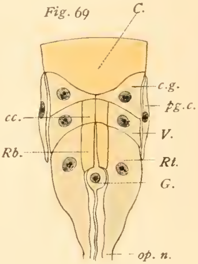

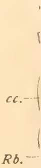

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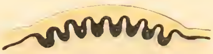

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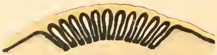

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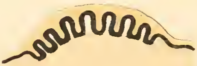
Fig 75



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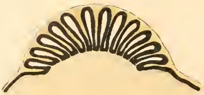

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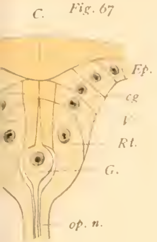

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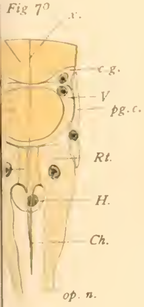

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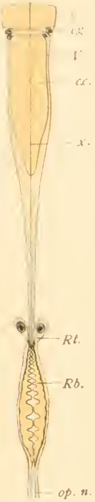

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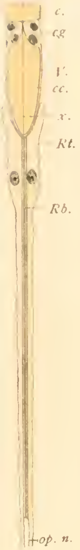

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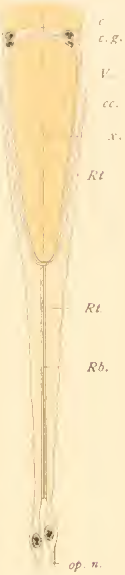

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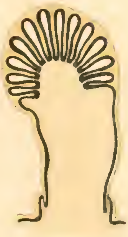
Fig. 79



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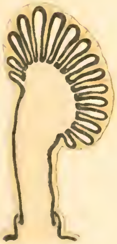

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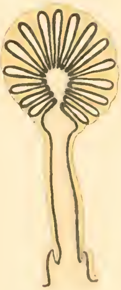

Shozaburo Watase.

I was born in the city of Tokio Japan in 1864. I took the degree of B.S., at the College of Sapporo, Japan in 1884. From 1884 – 1886 I devoted myself to the study of Zoology, at the Imperial University, Tokio, under Prof. K. Mitsukuri. In October 1886, I entered the Johns Hopkins University as a graduate student. My principal subject of study was Animal Morphology under Prof. W. K. Brooks; my first subsidiary was Comparative Psychology under Prof. G. Stanley Hall and Dr. H. H. Donaldson; my second subsidiary was Animal Physiology and Histology under Prof. H. N. Martin and Dr. H. W. Howell. By the permission of Prof. Marshal McDonald, I was enabled to spend three summers, (1887—1889) at the Woods Holl laboratory of U. S. Fish Commission for the study of marine Zoology in connection with my studies at the University laboratory in Baltimore.